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MAKING "HABITAT QUALITY" MEANINGFUL: QUANTIFYING DEMOGRAPHIC EFFECTS OF HABITAT IN TWO SYMPATRIC SPECIES

By

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Making “habitat quality” meaningful: quantifying demographic effects of habitat in two sympatric species

Chairperson: Paul M. Lukacs

Abstract

Habitat quality may be an underlying factor driving or exacerbating mule deer (*Odocoileus hemionus*) population declines across their range and concurrent white-tailed deer (*Odocoileus virginianus*) population increases. A clearer understanding of how the two species respond to habitat variables is needed to disentangle the drivers of mule deer decline and identify opportunities to change population trajectories through habitat management. Capitalizing on extensive monitoring data for sympatric populations of mule deer and white-tailed deer, this dissertation improves understanding of habitat quality by exploring and developing modeling approaches that connect habitat and demographics in these two species.

Using a resource selection function (RSF) in Chapter 1, I found a high degree of habitat overlap between mule deer and white-tailed deer and little support for niche differentiation between the two species during summer but not winter. Individual variation was strong and models were not predictive of future resource use. In contrast to the RSF, which assumes that resource selection corresponds with habitat quality, in Chapter 2 I used survival modeling to connect habitat to population performance. The survival model showed little connection between survival and winter severity, nutritional availability, or drought, suggesting that population-level survival of deer cannot be predicted by environmental conditions through these models. To overcome the limitations of current survival models, for Chapter 3 I developed a novel Survival and Habitat Quality model (SHQ) that directly estimates the effect of habitat on an individual’s unobservable survival probability. This autoregressive model allows inference to resources’ cumulative contribution to survival over an individual’s lifetime. Using the SHQ model in Chapter 4 for the first time, I estimated the long-term effects of habitat on survival. Unlike other survival models, the SHQ model was able to identify substantial differences between species and age classes in how environmental variables affected survival.

Together, these analyses build a more complete picture of habitat quality, selection, and use by sympatric ungulate species. The comparative investigation of methodologies can guide the selection of methodological approaches for species with comparable monitoring data. The improved approach developed in this dissertation will aid successful inference for conservation and management of many species.

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It is rare in ecology to have access to a dataset so extensive in spatial and temporal extent and with fine spatiotemporal resolution. I thank all the people from SDGFP who dedicated so many hours to organizing capture and monitoring collars, including Andy Lindbloom, Lauren Wiechmann, Andrew Norton, Steve Griffin, Sam Nichols, Gus Geldersma, Scott Stolz, Melinda Squillace, Bruce Bethea, Keith Mutschler, Colton Taylor, Garret Mooney, and numerous technicians and interns. I also thank the private landowners who made it possible to collar thousands of deer across South Dakota.

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A note on authorship

In the four chapters of this dissertation, I use the pronoun "we" in recognition and appreciation of the contributions of my collaborators and coauthors.

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Dissertation Introduction

All life forms need the right conditions to survive, grow, and reproduce, and populations can only persist where all these conditions are met. The set of biotic and abiotic conditions that can support a population’s existence determines patterns of species distributions (Morrison et al. 2006). Ecological theory and empirical studies show that low quality habitat supports smaller populations than high quality habitat (Fretwell and Lucas 1970, Pöyry et al. 2009, Häkkilä et al. 2018). Given that habitat loss and degradation are major concerns for wildlife species worldwide, understanding habitat quality is important for conserving wildlife populations (Maxwell et al. 2016, Horvath et al. 2019, Powers and Jetz 2019).

Defined as an individual's “per capita contribution to population growth expected from a given habitat,” habitat quality is extremely difficult to measure (Johnson 2007). This is because useful measures of habitat quality must connect habitat to long-term population trends, thus requiring large sample sizes and long-term datasets for precise estimation of survival, reproduction, and density (Van Horne 1983, Morrison et al. 2006). Only with clear estimates of these three demographic parameters over time and space can habitat quality be accurately quantified.

A number of different approaches have been designed to tackle the estimation of habitat quality. One of the most common approaches is the resource selection function (RSF), which estimates a species’ relative probability of use of different resources (Manly et al. 2002). RSFs assume that resource selection corresponds with habitat quality but does not connect habitat to population demographics. Survival modeling improves on this approach by connecting habitat to a demographic rate (survival). By relying on mortality locations to connect habitat to survival, survival modeling allows inference about resources on a relatively short time frame proximal to an individual's death. However, it provides no insight into how resources contribute cumulatively to survival over an individual's lifetime. An ideal habitat quality model would connect both the short- and long-term effects of habitat to population demographic rates such as survival.

Capitalizing on extensive monitoring data for sympatric populations of mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*), this dissertation aims to improve understanding of habitat quality by exploring and developing modeling approaches that connect habitat and demographics in these two species. Apparent declines of mule deer and increases of white-tailed deer populations in recent decades concern wildlife managers, and competition has been hypothesized as a possible driver (Anthony and Smith 1977, Whittaker and Lindzey 2004). Using this large dataset to understand the habitat quality needs of the two species will not only clarify the potential for competition and help managers design interventions to conserve mule deer but will also provide an opportunity to develop and test a new habitat quality modeling approach.

In Chapter 1, I use an RSF to measure resource selection at an individual scale using one of the largest global positioning system (GPS) collar datasets collected on sympatric mule and white-tailed deer. To improve understanding of habitat quality across time and space, Chapter 2 uses discrete-time survival modeling to measure spatial patterns in survival across populations using a 12-year dataset of 10 sympatric mule and white-tailed deer populations. In Chapter 3, I present and validate a new time-series habitat quality model that builds on existing methods and addresses the limitations of RSF and survival modeling from the first two chapters. Finally, Chapter 4 applies this novel survival-habitat quality model to our fine-scale GPS data to quantify the long-term effects of different resources on each deer species.

Together, these chapters provide insight into deer habitat needs for managers making decisions about habitat interventions to affect demographics of one or both species. They also provide a comparative investigation of different methodologies that can guide the selection of methodological approaches for species with comparable monitoring data. Conceptually and in practice, habitat quality is central to the work of both managers and researchers. The improved approach developed in this dissertation will aid successful inference for conservation and management of many species.

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Chapter 1. Comparative resource selection of two sympatric ungulate species in the northern Great Plains

Abstract

For decades, mule deer (*Odocoileus hemionus*) populations have appeared to shrink range wide, while white-tailed deer (*Odocoileus virginianus*) populations have increased, and their range has expanded. The underlying drivers of these patterns are unclear, and a combination of factors may be at play, including land use changes, climate change, and direct or indirect competition between the two species. Understanding how the two species share the landscape and whether niche partitioning exists would help shed light on the underlying drivers of mule deer decline and highlight opportunities to change population trajectories through habitat management. Using one of the largest GPS datasets ever collected on mule deer and white-tailed deer in their sympatric range, we used resource selection functions to investigate the relative probability of use of different resources available to the two species. Our models described population-level relative probability of use in winter and summer and demonstrated that a combination of factors, including nutrition, thermal cover, and human impact best described resource selection better than any single factor on its own. We verified patterns consistent with established patterns describing the two species' different uses of habitat and discovered some evidence of spatial segregation between mule deer and white-tailed deer. Inter-individual and intra-individual variation was high and made predictions of individual behavior and future patterns of resource selection difficult.

Introduction

For decades, biologists have noted the expansion of white-tailed deer (*Odocoileus virginianus*) range and abundance and the concurrent decline of mule deer (*Odocoileus hemionus*) abundance across their range (Wallmo 1981, VerCauteren 2003). Due to considerable range expansion of white-tailed deer westward and northward, the two species now have extensive range overlap in western North America (Hygnstrom et al. 2008). Many hypotheses have been proposed to explain the decline of mule deer and the increase of white-tailed deer, including differing effects of predators, weather, hunting, livestock, competition, disease, and habitat changes (Anderson et al. 2012, DeVivo et al. 2017). The observed success of white-tailed deer compared to mule deer could be an outcome of any of these hotly debated hypotheses.

Mule deer and white-tailed deer are habitat generalists, existing in a wide range of climates and vegetation communities; their sympatric range extends from Mexico to Canada. The two species' habitats are often differentiated from each other; white-tailed deer occupy habitats with more tree cover and agriculture whereas mule deer are expected in higher elevations and rangeland (Wood et al. 1989, Whittaker and Lindzey 2004). However, across their sympatric range the two species show a great deal of overlap in habitat selection and diet, leading many to conclude that they are direct competitors (Martinka 1968, Anthony and Smith 1977, Smith 1987, Lingle 2002, Whittaker and Lindzey 2004).

In the Great Plains, the relatively homogeneous habitat and lack of dramatic elevational gradients may increase the habitat overlap of mule deer and white-tailed deer, creating the potential for greater competition (Karish 2022). The relatively recent advent of global positioning system (GPS) collars and widely available, fine-grain remote sensing data have the potential to further disentangle resource selection between these two species in their sympatric range and provide additional evidence for patterns of habitat segregation and coexistence. Comparative resource selection can also help managers selectively manage habitats for species-specific management goals (Avey et al. 2003).

Research describing resource selection of mule deer and white-tailed deer follows some broad themes, three of which are nutrition, cover, and human impact. The first of these, nutrition, or access to forage, is probably the most commonly studied (Pierce et al. 2004, Whittaker and Lindzey 2004). Most studies on deer resource selection explore forage type, quantity, or quality as a driver of resource selection in some capacity (e.g., Haus et al. 1997, Pierce et al. 2004, Marshal et al. 2006, Jenkins et al. 2007, Kittle et al. 2008). Beyond using nutritional resources to describe a single species' patterns of resource selection, potential nutritional differences between the two deer species have long been sought to explain differences in their use of the landscape (Martinka 1968, Anthony and Smith 1977). Although the diets of mule deer and white-tailed deer are similar, differences in their nutritional needs and abilities to digest lower-quality forages may lead to differential resource selection between the species (Berry et al. 2019, Staudenmaier et al. 2022).

The second theme, cover, can be used to explain protection from predators (security cover) or the elements (thermal cover) including cold winters and hot summers (Pierce et al. 2004, Whittaker and Lindzey 2004). Differences in escape strategies from predators could influence the amount of cover needed for each species (Lingle 2002).

Critical temperature differences suggest that mule deer have a greater tolerance for low temperatures than white-tailed deer do but a similar heat tolerance (Parker and Robbins 1984, Mautz 1985). These physiological differences could lead to species-specific and season-specific selection of resources to meet their differing physiological needs.

Finally, human-impacted landscapes can affect deer both positively and negatively, and white-tailed deer may respond differently to human development than mule deer do. Areas of high urban development can act as refuges for both species and allow populations to become over-abundant (VerCauteren et al. 2005). In more rural areas, however, agriculture and roads are more predominant features of human impact that may affect resource selection of deer. Because white-tailed deer are often more associated with agriculture than mule deer, they may respond more positively to this aspect of human development. Furthermore, mule deer avoid highly modified areas such as well pads and high-traffic roads, thus establishing another difference between the two species (Sawyer et al. 2009).

Nutrition, cover, and human impacts can have different effects on deer resource selection throughout the year due to different habitat needs in different seasons (Long et al. 2009). First, dietary overlap of the two species in winter can be much greater than in summer, and the summer niche differentiation could be a mechanism for coexistence of the two species (Whittaker and Lindzey 2004). Second, because mule deer and white-tailed deer have similar heat tolerances but different cold tolerances, their selection for cover may be different between seasons (Mautz 1985, Parker and Gillingham 1990). Likewise, tolerance for human-impacted landscapes can change with weather or changes in human activities throughout the year. For example, mule deer avoid roads in summer but not winter (Marshal et al. 2006).

Using one of the largest GPS datasets of mule deer and white-tailed deer in their sympatric range ever collected, we compared resource selection between the species to identify habitat segregation in summer and winter. We compared four competing *a priori* ecological hypotheses driving resource selection: (1) access to nutrients and energy, (2) thermal cover, (3) human impact, and (4) multiple drivers (i.e., all of the above). We fit resource selection functions to two years of data to determine which hypothesis best described resource selection by mule deer and white-tailed deer, and we contrasted resource selection between seasons when deer may be driven by different biological needs. We also tested the ability of each hypothesis to predict future resource selection using a third year of data. In addition to comparing the predictive ability of the ecological hypotheses against each other, we compared them against an ecological null model to evaluate the overall quality of prediction (Koons et al. 2022).

Methods

Study area

We conducted the study in northwestern South Dakota, USA (Figure 1.1; 44°57'8" – 45°56'43" N, 100°18'31" – 104°2'44" W). In 2017, South Dakota Game, Fish and Parks defined 11 data analysis units (DAU) to designate deer populations for management and monitoring (South Dakota Department of Game Fish and Parks 2017). DAUs were defined by relatively homogeneous climate and geographic factors. Our study area, DAU 1 (~21,160 km^2), was dominated by mixed-grass prairie and agricultural crops. The 15-

year mean temperatures in this area ranged from -7°C in February to 23°C in August and mean precipitation ranged from 0.5 cm in January to 8.9 cm in May (National Climatic Data Center 2022). Elevation in the study area ranged from 490 m to 1173 m, and the land was a mixture of private and public ownership. In addition to mule deer and white-tailed deer, pronghorn (*Antilocapra americana*) were common, and elk (*Cervus canadensis*) were present but rare. Coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) were the most common and probable predators of deer.

Capture and collaring

Over the winters of 2019, 2020, and 2021, we captured and collared 345 mule deer and 345 white-tailed deer using helicopter net-gunning. We captured juveniles (<1 year-old) and adult females (>1 year-old). We aimed for even spatial representation of collars on both species across the study area and tried to spread collars across groups. We followed the American Society of Mammalogists' guidelines for animal capture and handling (Sikes et al. 2016), and our protocols were approved by University of Montana Institutional Animal Care and Use Committee (064-18PLWB-121418). Collars functioned for multiple years; collars recovered from mortalities were redeployed on new individuals. We outfitted each deer with a global positioning system (GPS) collar from Vectronic Aerospace GmbH (Berlin, Germany) or Telonics, Inc. (Mesa, Arizona, USA). The Vectronic collars used the Iridium satellite system and took positions every 5 hours (n = 135 deer). The Telonics collars used the GlobalStar satellite system and took positions every 5 hr (n = 81), 11 hr (n = 279), or 13 hr (n = 195). We placed non-expandable collars (495 – 560 g) on female deer, which we padded with temporary foam for juvenile females. On juvenile male deer, we deployed expandable collars (270 – 365 g) and temporary foam to allow for growth and neck expansion during the rut.

Home ranges

We designated mortalities that occurred within 14 days of capture as capture-related, and we excluded these individuals from analyses (Chalmers and Barrett 1982). We ignored GPS locations on the day of capture and the following day to remove potential effects of the helicopter capture on deer behavior. For any individuals that died during our study (not capture-related), we removed GPS locations from the two days prior to death to account for any uncertainty about timing of mortality. The GPS collars functioned for multiple years, so some individuals were represented in multiple years of our analysis (Table 1.1).

We created seasonal home ranges for each collared individual in winter (Jan – Mar) or summer (Jun – Aug) of 2019, 2020, and 2021 using 95% minimum convex polygons in R 4.1.3 (R Core Team 2022). Within each home range, we drew ten available locations for every recorded GPS location recorded for use in our resource selection function (Northrup et al. 2013).

Environmental variables

We used remote sensing data that have been developed and ground-truthed to quantify the resources at each used or available point. We chose independent predictor variables to represent our *a priori* hypotheses on habitat selection (Table 1.2).

For our nutrition hypothesis, we selected variables that we expected to be important food resources to deer, including shrubs (Carson and Peek 1987, Avey et al. 2003, Berry et al. 2019), perennial forbs and grasses (Martinka 1968, Berry et al. 2019), and important agricultural crops, including alfalfa (Martinka 1968), other hay, corn (Vercauteren and Hygnstrom 1998, Baasch 2008), soybeans (Baasch 2008), sunflowers (Kamler et al. 2009), spring wheat (Selting 1994), winter wheat (Thomas and Irby 1973), and other small grains (rye, barley, oats, and durum wheat). We first used the Rangeland Analysis Platform to quantify annual net primary productivity of shrubs (shrub NPP) and perennial forbs and grasses (perennial NPP) at 30m resolution (USDA Natural Resources Conservation Service et al. 2019, Robinson et al. 2019). Second, we used the annual 30m resolution crop cover layer from CropScape (USDA 2019) to classify lands into areas planted with the crops listed above. To capture all agricultural lands, including areas planted with crops not palatable to deer that would potentially be avoided, we classified all other cultivated areas not captured in these categories as "other crops". To differentiate between agriculture and non-agriculture lands, we designated uncultivated areas as the category "no crops".

To represent thermal cover and exposure for our second hypothesis, we used variables representing tree cover and shelter from the wind. We obtained percent tree cover at 30 m resolution from the Rangeland Analysis Platform. To represent shelter from the wind, we first created a categorical variable for direction of exposure. To classify direction of exposure, we calculated aspect from the 10m resolution The National Map Digital Elevation Model (U.S. Geological Survey 2019) using Google Earth Engine (Gorelick et al. 2017), then we created four bins: east (between 45° and 135°), south (between 135° and 225°), west (between 225° and 315°), and north (between 315° and 45°). Additionally, we calculated slope from The National Map to help quantify thermal shelter, as more complex terrain (i.e., greater slopes) may provide micro-climate refuges from wind in the Great Plains. Finally, we represented a component of thermal shelter by classifying lands that were enrolled in the Conservation Reserve Program (CRP) and allowed to grow without annual grazing or mowing (Selting 1994). We obtained a polygon dataset of lands enrolled in CRP in 2020, and we removed enrolled parcels that allowed annual grazing or haying (i.e., practices “CP87”, “CP87A”, “CP88”, and “CP88A”; Farm Service Agency 2020). For the purposes of making predictive maps, we created a 30 m resolution raster from this polygon dataset.

To represent human impact, we used a conglomerate human modification score as well as road density. The global Human Modification (gHM) dataset provides a 0-1 score for each 1000 x 1000m cell worldwide, and it represents the proportion of each cell that has been modified and the intensity of modification due to human settlement, agriculture, transportation, mining and energy production, and electrical infrastructure (Kennedy et al. 2019). Because agriculture was a component of this calculation, we chose to let that component of gHM represent the coarse-grain process of land conversion, while the crop variables in our nutritional model represented finer-grain selection or avoidance of particular crops. Additionally, although roads were captured at a large scale by gHM, we also calculated road density at a 30 m resolution to capture finer-grain detail of the study area, using the TIGER US Census roads dataset (United States Census Bureau 2016) and Google Earth Engine.

We centered and scaled all continuous covariates to assist with model convergence and allow for direct comparison of parameter estimates. The variables we used were not strongly collinear ($R^2 < 0.6$ for all pairs).

Resource selection function

We used logistic regression to model third-order resource selection (use of habitats within home range) from our used-available design (Johnson 1980, Manly et al. 2002, Thomas and Taylor 2006). This approach allowed us to estimate the exponential resource selection function and relative probability of use of different resources (Lele and Keim 2006). To account for inter-individual differences in habitat selection behavior and data collection (e.g., fix rate), we used a random intercept for individual in all models. When fitting the generalized linear mixed models using R package glmmTMB version 1.1.3 (Brooks et al. 2017), we assigned a weight of 1 for used points and a weight of 5,000 for available points, and we fixed the variance of the random intercept at 1,000 (Muff et al. 2020).

We fit five models separately for mule deer and white-tailed deer in winter and summer (Table 1.2). We used the sample-size corrected Akaike's Information Criterion (AICc) to assess relative support of our ecological hypotheses and select the most parsimonious model (Burnham and Anderson 2002) for each species, season, and year. We also assessed model fit and predictive power using two methods. Our first method was out-of-sample validation using root mean squared error (RMSE). For each of the first two years of data (2019 and 2020), we randomly selected 20% of the individuals to withhold, and we fit each model to the other 80%. We calculated RMSE on the withheld

20% of individuals; this represented a measure of within-year validation. We also tested prediction ability (hereafter called “next-year validation”) by fitting the model to the following year’s used and available data and calculating RMSE. Our second method of validation was Spearman-rank correlation (Boyce et al. 2002). After fitting the RSFs and using AICc to select the top model, we created predictive maps of resource selection based on the top model for each species, season and year. We then collected the values into 10 equal-area bins. Spearman-rank correlation quantifies the correlation between the number of used points in each bin to the bin rank (1 through 10), with 1 representing high predictive performance and 0 representing low performance. We quantified within-year validation via Spearman-rank correlation using that year’s used locations, and we calculated next-year validation by using the following year’s locations. For within-year and next-year validation, we calculated Spearman-rank correlation at the population level by pooling all individuals’ locations and at the individual-level by classifying the count of locations in each bin separately by individual.

Results

Landscape inventory

Our study area was predominantly non-agricultural, with 87 – 88% of the study area categorized as “no crops” each year (Table 1.3). CRP land that wasn’t mowed or grazed annually represented only 1% of our study area. Of the crops grown, other hay (excluding alfalfa) was the most common, and soybeans and winter wheat were the least common. Of our continuous variables, values of road density and NPP of perennial forbs and grasses were approximately evenly distributed on both sides of the median, whereas percent tree cover, slope, and shrub NPP were highly skewed (Table 1.4, Figure 1.2). The skew showed that the majority of values recorded in our study area were small, but some values were very large compared to the mean.

Model selection

For seven of our eight species-season-year combinations (mule deer and white-tailed deer, winter and summer, 2019 and 2020), the global model was the most parsimonious as determined by AICc (Table 1.5). For each of these seven, the global model received 100% of the model weight, suggesting that none of the other four models (nutrition, thermal, human impact, or null) should be considered as a contender for explaining resource selection. However, for resource selection of mule deer in summer 2019, the nutrition and global models did not converge; the variance-covariance matrices were not estimable. Therefore, these two models were excluded from further consideration (Brooks et al. 2022). Of the three models that converged for mule deer summer 2019, the thermal model received 100% of the model weight.

Mule deer

We used the top model for summer and winter of each year to identify patterns in mule deer seasonal resource selection (Figure 1.3). Mule deer selected for CRP lands in the winter but avoided or showed no response to them during the summer. Mule deer in winter of both years showed selection for soybeans, corn, alfalfa, spring wheat, and “other” crops. Of these, corn, spring wheat, and other crops were also selected in summer, but soybeans and alfalfa were neither selected nor avoided. Mule deer had inconsistent selection of other non-alfalfa hay and sunflowers; in the first winter these crops were neither selected nor avoided, but they were both selected in the next winter. The first of these, non-alfalfa hay, was avoided in the summer, whereas sunflowers were selected year-round in 2020 (no estimate was available for summer 2019 in the top model). In one winter, mule deer appeared to avoid winter wheat, but the next winter they showed no selection or avoidance, and in one summer they selected winter wheat. Selection of aspect was different between winter and summer; in winter, northern aspects were avoided and southern aspects were selected, but in summer, northern aspects were selected and southern aspects were neither selected nor avoided. Mule deer selected for lands with high human modification in the winter but avoided them in summer, and selection for road density was inconsistent between seasons and years. Additionally, selection for percent tree cover was inconsistent; in the first summer and following winter, tree cover was selected, but in the other seasons it was neither selected nor avoided. Finally, mule deer displayed year-round selection for steeper slopes and higher shrub NPP and perennial NPP.

White-tailed deer

Compared to mule deer, white-tailed deer had consistent positive selection across seasons and years for a greater number of environmental variables. These included year-round selection of corn, soybeans, spring wheat, other small grains, “other” crops, higher human modification, higher road density, higher perennial NPP, higher shrub NPP, steeper slopes, and higher percent tree cover (Figure 1.3). Like mule deer, white-tailed deer showed varied responses to alfalfa, winter wheat, and other hay across seasons and years. Also similar to mule deer, white-tailed deer also had a positive or neutral response to sunflowers in each season. As with mule deer, white-tailed deer avoided northern aspects and selected for southern aspects in the winter, but in contrast to mule deer, they had more varied responses to aspect in the summer. Finally, white-tailed deer showed no consistent response to CRP; they selected and avoided CRP in the two winters, and they selected or showed no response in the summers.

Species comparison

Overall, white-tailed deer responded consistently between seasons and years to more resources than mule deer did. However, the two species showed consistent, positive, year-round selection of quite a few variables, including corn, spring wheat, other crops, slope, shrubs, and perennials. They both selected southern slopes in the winter and avoided northern slopes. Furthermore, both species responded positively to human modification and road density in winter, although they had opposite responses in the summer, with mule deer appearing to avoid areas of higher human modification and road density in summer and white-tailed deer selecting them. These were the only two variables that provided evidence of spatial partitioning in summer but not winter, although the evidence was weak because the top model for mule deer in the first summer did not have parameter estimates for these variables.

Model fit and prediction ability

We validated all ecological hypotheses using RMSE for within-year fit and next-year prediction, and we validated the top model for each species, season, and year using Spearman-rank correlations. For within-year fit from RMSE, the global model was generally ranked last and the null model was ranked first (Table 1.6). This contrasted with model selection by AICc, which ranked the global model first (Table 1.5). Next-year fit from RMSE showed that all models performed approximately equally, although once again the global model was frequently ranked last and the least complex models (null and human impact) were ranked first in predictive ability (Table 1.7).

At the population level, we found very high Spearman-rank correlation ($r \geq 0.92$) between RSF value and predicted within-year use and next-year use for all of the following: mule deer in summer of both years, white-tailed deer in winter of both years, and white-tailed deer in summer 2020 (Table 1.8). Mule deer had slightly lower scores ($r \geq 0.84$) in winter of both years. For each of these seven species-season-year combinations, within-year fit was greater than or approximately equal to next-year fit. In contrast, RSF values for white-tailed deer in summer 2019 had much lower correlation with use than any of the other models, and within-year correlation ($r = 0.37$) was less than next-year correlation ($r = 0.45$).

Model performance at the individual level was worse than population-level performance for all models (Table 1.8). This indicated that individuals' patterns of selection were more variable than the overall population's pattern of selection. Furthermore, the models did not consistently perform better at estimating an individual's relative probability of use of different resources within a year than across years. This indicated that variation in selection was common within a single individual across time.

We created predictive maps of resource selection for each species, season, and year using the top model selected by AICc (Figure 1.4). RSF values were grouped into 10 equal-area bins for visualization. Because population-level Spearman-rank correlation was generally high, the maps illustrate the relative probability of use spatially distributed in our study area (Boyce et al. 2002).

Discussion

Overall, we found some evidence of spatial segregation between mule deer and white-tailed deer due to their patterns of resource selection. Consistent with long-established patterns, white-tailed deer selected for agriculture and tree cover more consistently than mule deer did (Whittaker and Lindzey 2004, Baasch 2008). However, both species responded positively to many different crops, perennial NPP, and shrub NPP, which was evidence of a large degree of overlap in diet (Anthony and Smith 1977, Smith 1987, Whittaker and Lindzey 2004, Baasch 2008, Karish 2022). Additionally, there was little evidence of a greater degree of habitat overlap during winter than summer. In support of this idea and the hypothesis that summer niche differentiation is a mechanism for coexistence (Whittaker and Lindzey 2004), resource selection was similar between the two species in winter but different in summer for soybeans, northern aspects, and human impact. However, for all other environmental variables, the two species had similar selection year-round or selection was highly variable between seasons and years (Figure 1.3). Deer populations in our study area were not migratory, and niche differentiation between seasons may be weaker when summer and winter ranges are not distinct.

There was mixed support for our hypothesis that the combination of nutrition, thermal cover, and human impact described resource selection better than any of the three on its own. On one hand, this model was consistently selected by AICc and had high predictive ability for population-level relative probability of use (Table 1.8). On the other hand, it never outperformed the ecological null model (selection is in proportion to availability) for prediction of resource selection by individuals not used to fit the model (Tables 1.6 – 1.7). Several factors may be responsible for these results. First, large sample sizes can lead to AIC selection of more complex models (Boyce et al. 2002). This is because large sample sizes can support precise estimates of very small effects – thus leading to selection by AIC – but if the variance in responses is large compared to the effect size, prediction ability suffers. Second, many of our variables were uncommon on the landscape (Tables 1.3 – 1.4), and selection strength would need to be very high to drive animals to use those resources more than the common resources. Third, our two species were habitat generalists, and predictions from resource selection functions are less robust for generalists than for habitat specialists because RSFs do not account for individual variation (Boyce et al. 2002, Montgomery et al. 2018).

Our results showed a high degree of habitat generalism for the two species; inter-individual variation within a year and intra-individual variation across years were high, so the models did not apply well to different individuals or different times. We determined there was high inter-individual variation by Spearman-rank correlation. Although selection by the population as a whole may have been predictable by the model, any one individual's pattern of selection was not (Table 1.8). We also suspect that intra-individual variation was high across years; individuals that lived multiple years were used both to fit the model and validate the model to the following year's used locations. However, this did not improve prediction between years, and in fact next-year prediction was often worse than prediction to other individuals within a year. High intra-individual variation was not likely caused by a dynamic landscape; there was little variation in the makeup of our study area between years (Tables 1.2 – 1.3, Figure 1.2). Furthermore, we do not suspect that the landscape context (i.e., the spatial arrangement of resources) changed greatly between years, as our only temporally varying resources were crops, tree cover, and NPP, which would only be expected to vary at the scale of the land ownership.

Although the support for our models as predictors was mixed, the top models selected by AIC were highly successful at describing relative probability of use at the population scale (Table 1.7). Therefore, they served as good descriptors of resource selection and relative probability of use at the population scale during the years used to fit the models, even though predictive ability was limited. Thus, we interpreted the selection coefficients from the top models to evaluate the support for selection of different resources within the categories of nutrition, thermal cover, and human impact. Overall, the selection coefficients from our top models indicated that nutrition was an important driver of resource selection and that thermal cover and human impact drove some species-specific differences in resource selection between seasons.

First, we found evidence of dietary overlap and the importance of nutrition on resource selection by the responses of mule deer and white-tailed deer to shrubs, perennial forbs and grasses, and crops. Both species showed small but consistent selection for shrubs and perennial forbs and grasses throughout the year. Additionally, both species showed positive year-round selection of corn, spring wheat, and other crops, and white-tailed deer also had positive year-round selection of soybeans and other small grains. Because selection was positive in all seasons, these crops may be vulnerable to depredation most consistently of any crop in our study area. However, the strength of selection for these crops was not notably greater than for other crops, so their relative probability of use may not have been greater than for other crops.

Second, we found support that thermal cover was important for resource selection. In winter, both species showed avoidance of north-facing slopes and selection for south-facing slopes, which receive more solar radiation. They both selected positively for steeper slopes year-round, which represented terrain complexity and potential wind refuges in our relatively flat study area. Steeper slopes were associated with two main features: river bottoms and buttes. White-tailed deer may have predominantly selected the former while mule deer selected the latter, which would be consistent with previous descriptions of habitat differentiation between the two species. White-tailed deer consistently selected for higher percent tree cover in summer and winter, whereas mule deer sometimes selected for higher percent tree cover and sometimes did not. The effect sizes for selection of tree cover were very small, which may be because trees were uncommon in our study area (Table 1.4). Deer response to CRP was not consistent across years or seasons for either species, except mule deer selected for CRP in both winters. Responses to CRP can be highly variable, and it may be more important in other times of year (e.g., parturition) than winter or summer (Thomas and Irby 1973, Gould and Jenkins 1993, Selting and Irby 1997, Kern 2019). Overall, the responses to different aspects of thermal cover indicated that resource selection was more similar between the two species in winter than in summer, which did not support our hypothesis that selection would be driven by different lower critical temperatures between species but similar upper critical temperatures.

Third, for human impact, we found some species-specific and season-specific patterns. Our study area was rural with no major urban interfaces, so the biggest feature of human modification was agriculture. Both species of deer responded positively to human modification in winter, and white-tailed deer maintained positive selection in summer, but mule deer avoided human modification in summer. Additionally, we found that white-tailed deer selected for areas with higher road density year-round, whereas – consistent with prior literature – mule deer selected these areas in the winter but avoided them in summer (Marshal et al. 2006). Because our study area was so rural, roads were mostly low-speed roads through agricultural land. This could indicate that positive selection was for agriculture, which happened to coincide with higher road density, but avoidance by mule deer in summer could have been driven by either avoidance of roads or agriculture. Together, these results indicated that white-tailed deer had a higher tolerance for human activity, and the results could potentially highlight a small amount of spatial partitioning between the species.

Assuming resource selection correlates with a demographic benefit to the populations, our results do not point to any clear management actions that could be taken to benefit mule deer more than white-tailed deer. No single resource was consistently selected by one species and avoided by the other in winter or summer. Furthermore, effect sizes across variables were typically small or imprecisely estimated, and no variable stood out with a consistent, outsized effect on resource selection (Figure 1.3). Small effect sizes indicated resources were selected slightly out of proportion with their availability, and without measuring a demographic benefit (i.e., increased fitness due to resource use), we could not tease apart whether these resources were of small importance or highly important but only in small amounts.

Our extensive GPS collar dataset allowed closer examination of resource selection and differentiation by mule deer and white-tailed deer in their sympatric range at a large spatial extent and fine spatial grain. We found evidence that resource selection of both species was driven by a combination of factors, including nutrition, thermal cover, and extent of human impact. However, even with one of the largest datasets ever collected on these two species, we were not able to overcome high levels inter-individual variation to make generalizable conclusions about the resource needs of these two generalist species. The inability of our models to accurately predict future resource selection by individuals demonstrates that predicting habitat use and measuring habitat quality is more complex than resource selection function modeling allows. Furthermore, using the RSF approach we had to assume a demographic benefit of resource selection, but without measuring this more directly, we encourage caution in making habitat management decisions based on resource selection. To connect resources on the ground to demographic performance of a population, the next step is understanding spatial patterns in survival, which we address in Chapter 2.

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Tables

Table 1.1. Number of individuals with GPS collars used in RSF analyses by species, season, and year.

	2019	**2020**	**2021**
Mule deer winter	102	202	222
Mule deer summer	92	131	153
White-tailed deer winter	101	205	218
White-tailed deer summer	88	159	172

Table 1.2. Variables used in resource selection. All models contained a random effect for individual ID.

Model	
Nutrition	crops [alfalfa] + crops [corn] + crops [other hay] + crops [other small grains] + crops [other crops] + crops [soybeans] + crops [spring wheat] + crops [sunflower] + crops [winter wheat] + perennial NPP + shrub NPP
Thermal	tree % cover + direction [north] + direction [west] + direction [south] + CRP + slope
Human impact	human modification + road density
Multiple drivers	crops [alfalfa] + crops [corn] + crops [other hay] + crops [other small grains] + crops [other crops] + crops [soybeans] + crops [spring wheat] + crops [sunflower]+ crops [winter wheat] + perennial NPP + shrub NPP + tree % cover + direction [north] + direction [west] + direction [south] + CRP + slope + human modification + road density
Null	Intercept only

Table 1.3. Percentage of study area represented by each categorical variable. Some values varied by year and are shown by ranges.

Environmental variable	Percentage of study area
Direction [N]	24%
Direction [S]	25%
Direction [W]	23%
CRP	1%
Crops [Alfalfa]	2-3%
Crops [Corn]	2%
Crops [No crops]	87-88%
Crops [Other small grains]	0-1%
Crops [Other crops]	1-2%
Crops [Other hay]	6-7%
Crops [Soybeans]	0%
Crops [Spring wheat]	3%
Crops [Sunflower]	1-2%
Crops [Winter wheat]	0%

Table 1.4. Values of continuous variables in study area.

Variable	Year	Percentile	Value
Slope (°)	all	minimum	0
	all	median	2.24
	all	maximum	88
Human modification (0-1)	all	minimum	0
	all	median	0.1
	all	maximum	0.68
Road density (%)	all	minimum	0.54
	all	median	0.75
	all	maximum	0.96
Tree cover (%)	2019	minimum	0
		median	0
		maximum	96
	2020	minimum	0
		median	0
		maximum	96
	2021	minimum	0
		median	0
		maximum	96
Perennial NPP (g C m^{-2} yr^{-1})	2019	minimum	0
		median	3248
		maximum	6414
	2020	minimum	0
		median	2703
		maximum	6284
	2021	minimum	0
		median	2159

		maximum	5609
Shrub NPP (g C m^{-2} yr^{-1})	2019	minimum	0
		median	19.2
		maximum	1244
	2020	minimum	0
		median	0.59
		maximum	1025
	2021	minimum	0
		median	0.22
		maximum	909

Table 1.5. Model selection by AICc.

	Model	AICc	ΔAICc	Model weight	K
Mule deer winter 2019	Global	386922	0	1	20
	Thermal	388493	1571	0	7
	Nutrition	390542	3620	0	12
	Human impact	392529	5607	0	3
	Null	392699	5777	0	1
Mule deer winter 2020	Global	755145	0	1	20
	Thermal	757696	2550	0	7
	Nutrition	759512	4366	0	12
	Human impact	760704	5558	0	3
	Null	761356	6210	0	1
Mule deer summer 2019	Global*	-	-	-	20
	Thermal	414500	0	1	7
	Nutrition*	-	-	-	12
	Human impact	416660	2159	0	3
	Null	416743	2243	0	1
Mule deer summer 2020	Global	583103	0	1	20
	Thermal	586815	3712	0	7
	Nutrition	588620	5517	0	12
	Human impact	591879	8777	0	3
	Null	592012	8909	0	1
White-tailed deer winter 2019	Global	368416	0	1	20
	Thermal	370394	1978	0	7
	Nutrition	370791	2375	0	12
	Human impact	371286	2870	0	3
	Null	372369	3953	0	1
White-tailed deer winter 2020	Global	770925	0	1	20
	Nutrition	773182	2257	0	12
	Human impact	774820	3895	0	3
	Thermal	775034	4109	0	7
	Null	776296	5371	0	1
White-tailed deer summer 2019	Global	362200	0	1	20
	Nutrition	363019	819	0	12
	Thermal	365613	3413	0	7
	Human impact	366842	4642	0	3
	Null	366995	4795	0	1
White-tailed deer summer 2020	Global	704089	0	1	20
	Nutrition	705619	1530	0	12
	Thermal	716892	12803	0	7
	Human impact	719026	14937	0	3
	Null	719356	15267	0	1
*Model did not converge and removed from consideration					

Table 1.6. Root mean squared error (RMSE) of within-year out-of-sample validation for resource selection models. The best predictive model (lowest RMSE) for each species and season is highlighted in blue, and the worst predictive model is in red.

	Nutrition	Thermal	Humans	Global	Null
Mule deer winter 2019	0.38	0.53	0.4	0.59	0.3
Mule deer winter 2020	0.39	0.41	0.41	0.56	0.3
Mule deer summer 2019	-	0.35	0.34	-	0.3
Mule deer summer 2020	0.61	0.48	0.38	0.83	0.3
White-tailed deer winter 2019	0.4	0.37	0.43	0.57	0.3
White-tailed deer winter 2020	0.46	0.35	0.41	0.56	0.3
White-tailed deer summer 2019	0.75	0.35	0.33	0.82	0.3
White-tailed deer summer 2020	0.86	0.34	0.34	0.87	0.3

Table 1.7. Root mean squared error (RMSE) of next-year prediction for resource selection models. Models were fitted to one year of data and tested on the following year’s used and available points. The best predictive model (lowest RMSE) for each species and season is highlighted in blue, and the worst predictive model is in red.

	Nutrition	Thermal	Humans	Global	Null
Mule deer winter 2019	7.12	7.13	7.03	7.24	7.03
Mule deer winter 2020	7.64	7.55	7.55	7.72	7.53
Mule deer summer 2019	-	7.49	7.46	-	7.46
Mule deer summer 2020	8.34	8.09	8.03	8.44	8.03
White-tailed deer winter 2019	7.04	7.00	7.01	7.10	6.96
White-tailed deer winter 2020	7.66	7.54	7.53	7.68	7.53
White-tailed deer summer 2019	7.17	6.91	6.90	7.17	6.90
White-tailed deer summer 2020	8.34	7.86	7.82	8.35	7.83

Table 1.8. Spearman rank for top model of each species, season, and year, validated within year and to next year, as well as population-wide and individual-based.

Season	Species	Year	Validation year	Spearman rank - population	Spearman rank - individual
Winter	Mule Deer	2019	within	1.00	0.35
Winter	Mule Deer	2019	next	0.84	0.10
Winter	Mule Deer	2020	within	0.89	0.17
Winter	Mule Deer	2020	next	0.87	0.31
Summer	Mule Deer	2019	within	0.99	0.71
Summer	Mule Deer	2019	next	1.00	0.51
Summer	Mule Deer	2020	within	1.00	0.46
Summer	Mule Deer	2020	next	1.00	0.59
Winter	White-tailed Deer	2019	within	1.00	0.61
Winter	White-tailed Deer	2019	next	0.92	0.37
Winter	White-tailed Deer	2020	within	0.96	0.48
Winter	White-tailed Deer	2020	next	0.99	0.56
Summer	White-tailed Deer	2019	within	0.37	0.19
Summer	White-tailed Deer	2019	next	0.45	0.11
Summer	White-tailed Deer	2020	within	0.99	0.45
Summer	White-tailed Deer	2020	next	0.96	0.51

Figures

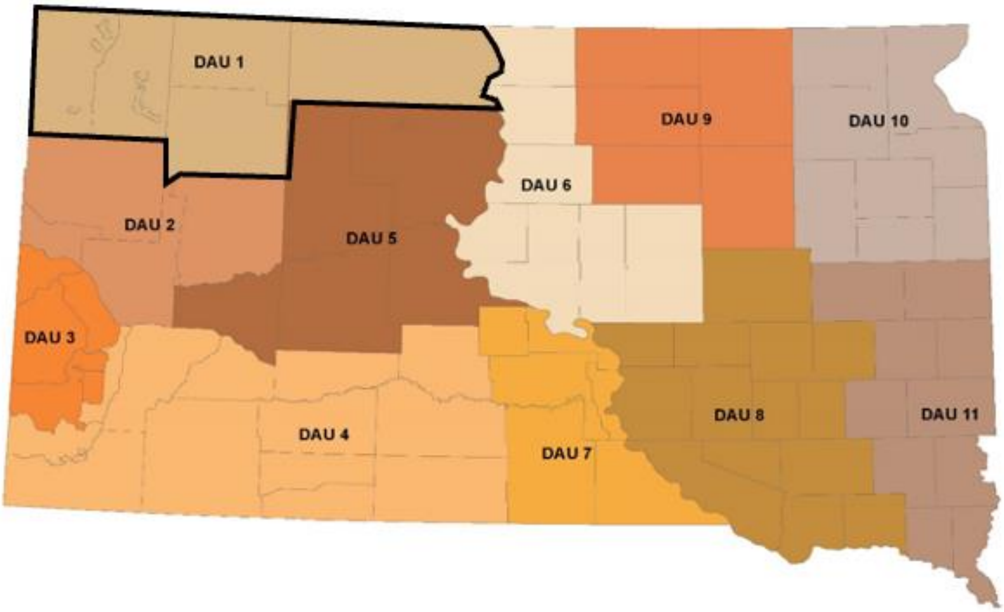

Figure 1.1. Data analysis units (DAUs) in South Dakota, USA, with our study area, DAU 1, outlined in black.

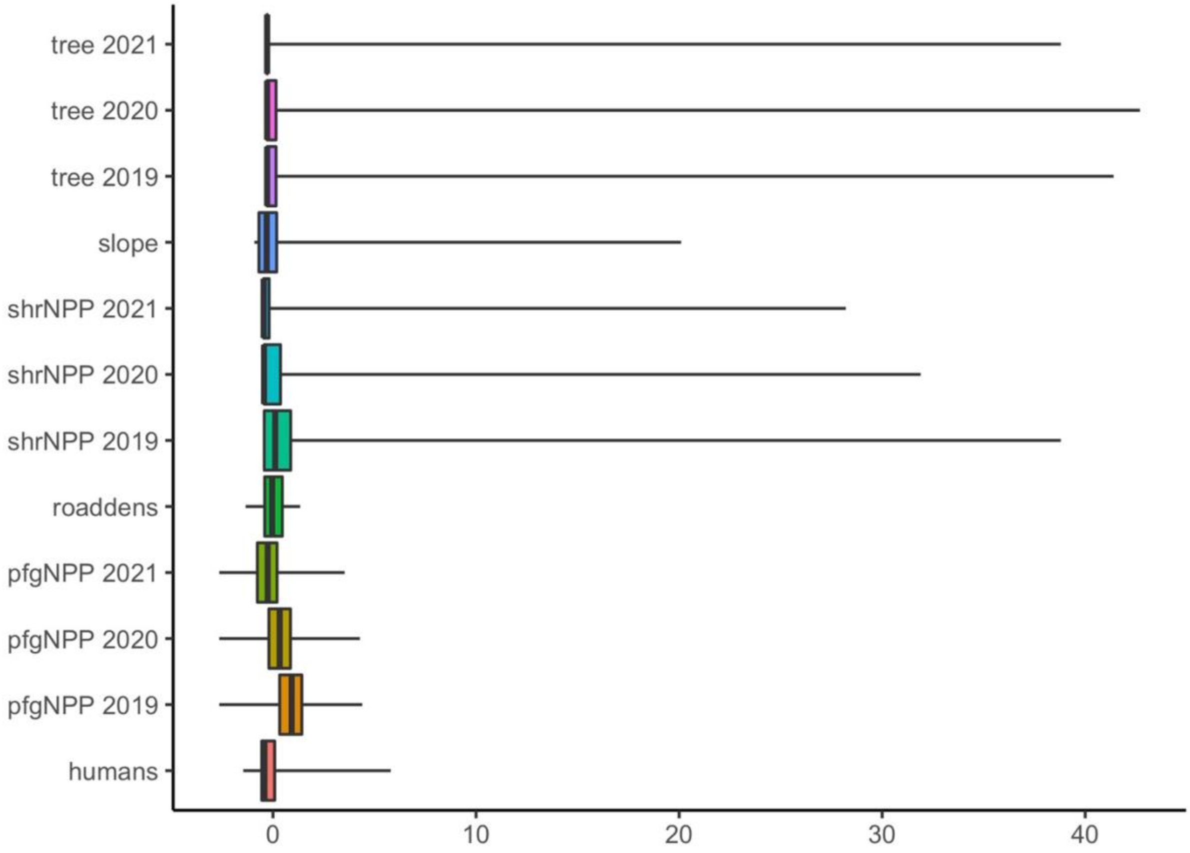

Figure 1.2. Interquartile ranges of centered-and-scaled continuous covariates in our study area. Horizontal lines (whiskers) span minimum and maximum values, boxes span 25th to 75th percentiles, and vertical lines mark median values.

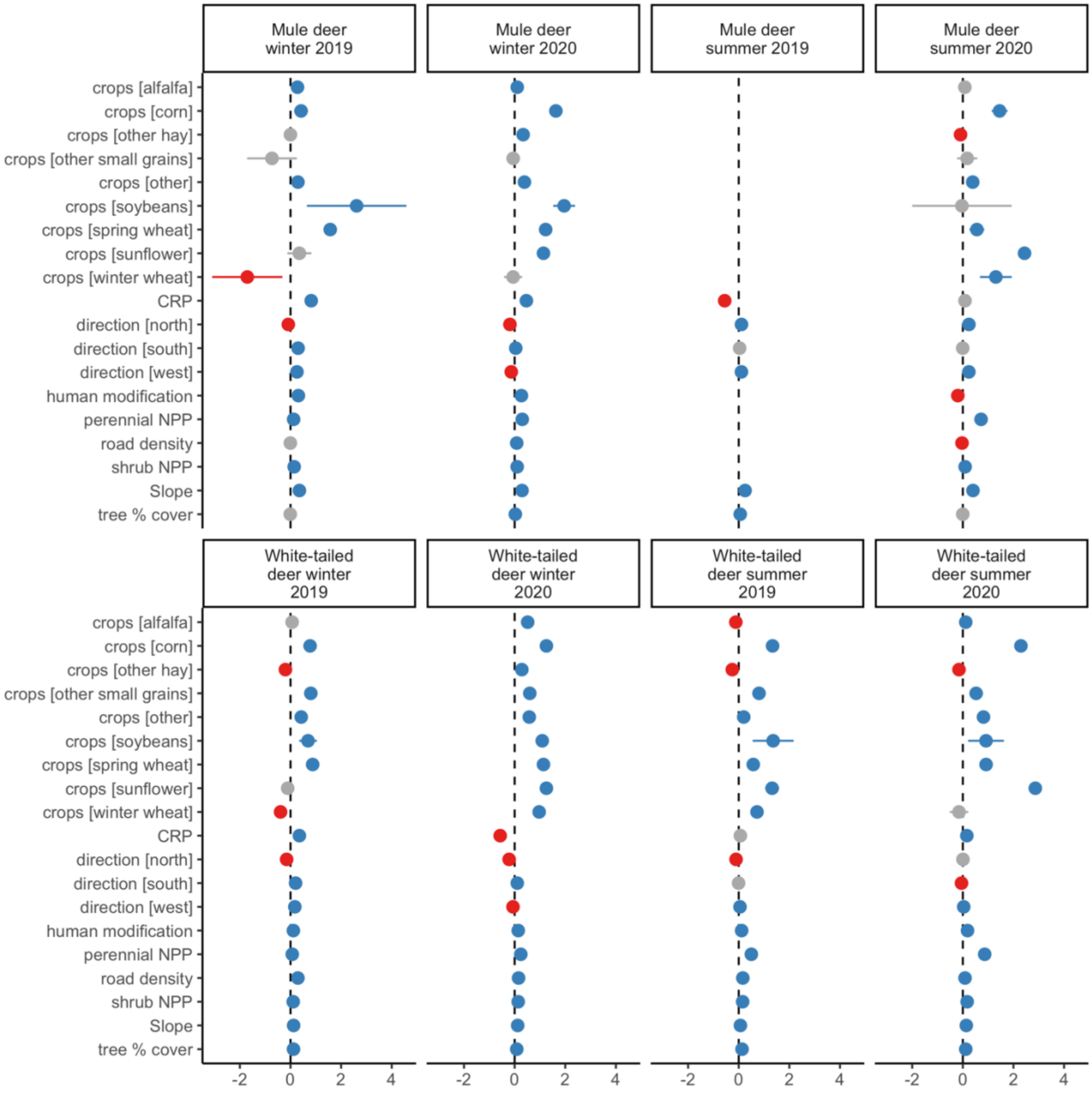

Figure 1.3. Selection coefficients and confidence intervals (horizontal bars) for different resources by mule deer and white-tailed deer in winter and summer of two different years, as estimated by the top model for each. Negative effects shown in red, positive effects shown in blue, and no effect (95% confidence interval crosses 0) shown in gray.

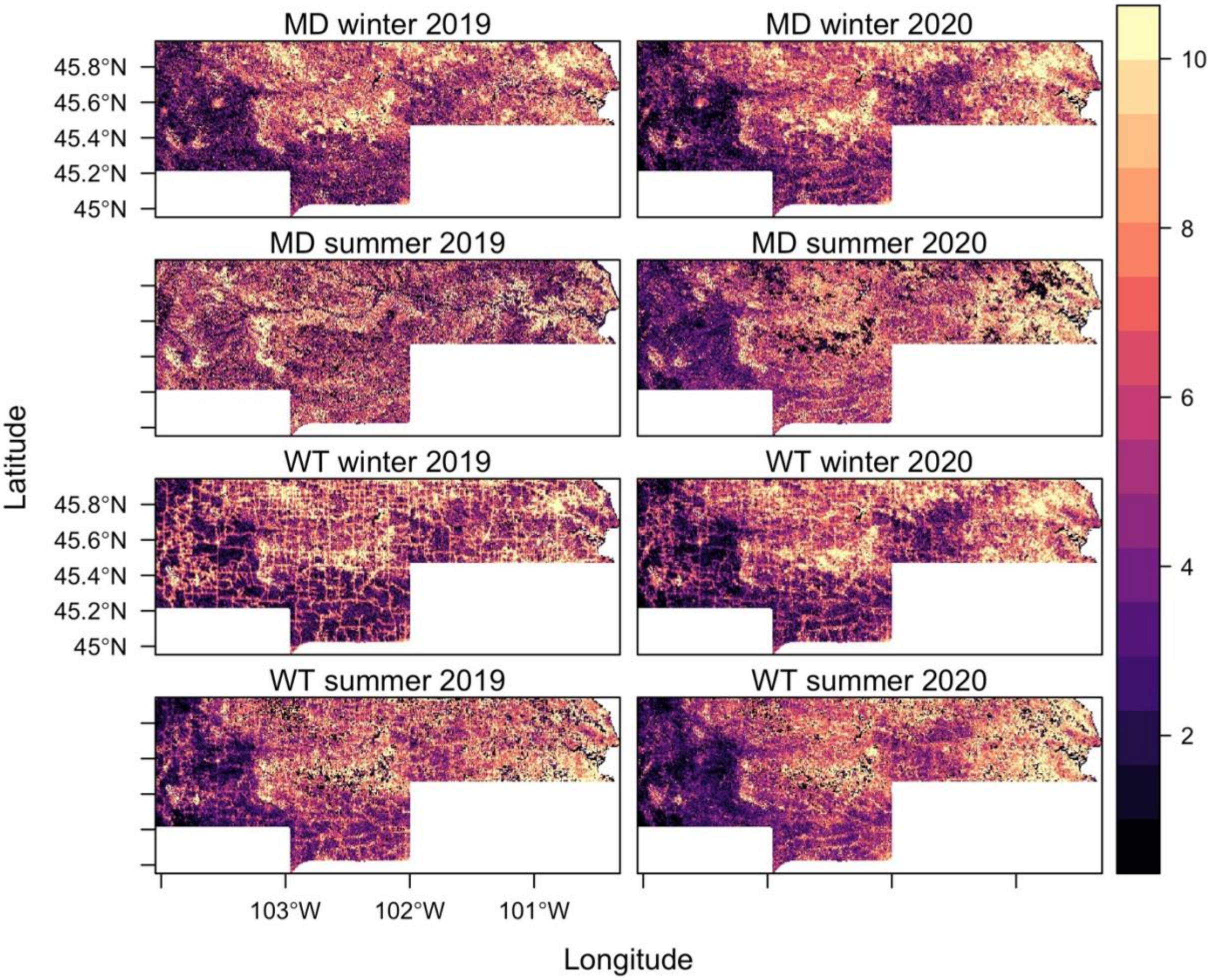

Figure 1.4. Maps of resource selection in northwestern South Dakota for winter and summer of 2019 and 2020 for mule deer (MD) and white-tailed deer (WT). Colors represent binned RSF values from low relative probability of use (1) to high relative probability of use (10).

Chapter 2. Applying a Bayesian ragged telemetry model to quantify environmental influences on survival of mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*)

Abstract

Environmental factors that differentially influence survival of mule deer and white-tailed deer could help explain the range expansion and population increases of white-tailed deer while mule deer populations decline. Because mule deer and white-tailed deer are long-lived species as well as habitat generalists, estimating environmental effects on survival requires large numbers of individuals over long timeframes. Such datasets often contain multiple types of monitoring information, and often include both very high frequency (VHF) and global positioning system (GPS) collars, which contain different information and levels of uncertainty. Using a Bayesian ragged telemetry model originally proposed to estimate avian nest survival, we integrated VHF and GPS collar data for 10 populations of sympatric mule deer and white-tailed deer over 12 years. We tested three hypothesized drivers of monthly survival for juvenile and adult deer: (1) harsh winters decrease survival; (2) nutrient availability increases survival; (3) drought decreases survival. We found little evidence consistent with any of our three hypotheses and concluded that population-level survival of deer cannot be predicted by environmental conditions.

Introduction

Over recent decades, mule deer (*Odocoileus hemionus*) range and abundance have declined while white-tailed deer (*Odocoileus virginianus*) range and abundance have increased (Wallmo 1981, VerCauteren 2003). The two deer species have much in common: they are long-lived ungulates and habitat generalists, and they exist in a wide range of climates and vegetation communities, including an extensive overlapping range in North America (VerCauteren 2003). However, mule deer and white-tailed deer have slightly different life histories; mule deer tend to have higher adult survival than white-tailed deer but take longer to mature to reproductive age (Nixon 1971, Mueller and Sadleir 1979, DeYoung 2011, Forrester and Wittmer 2013). The small but meaningful differences in population dynamics may indicate that environmental and habitat conditions affect the two species differently. These differences are particularly important to understand in the two species' sympatric range, where many biologists are concerned about the future of mule deer populations.

Deer survival can be affected by environmental conditions, and the two species may have different tolerance levels for harsh conditions. Our goal was to understand the environmental conditions that affect survival of mule deer and white-tailed deer in their sympatric range. We explored three hypotheses to explain and predict survival of different ages and sexes of both species. We hypothesized that (1) harsh winters decrease survival; (2) nutrient availability increases survival; (3) drought decreases survival.

The first hypothesis, winter severity, has long been proposed as a limiting factor on deer survival for a variety of reasons. First, deep snow requires more energetic expenditure and leads to reduced survival in adults and juveniles (Moen 1976, Parker et al. 1984, Jackson et al. 2021). Second, nutrition is limiting in the winter (Bishop et al. 2009, Bergman et al. 2014), and limited access to nutrition caused by snow cover may lead to poorer body condition and therefore to lower survival. Third, when environmental conditions expose deer to temperatures below their critical body temperature, deer must expend additional energy to stay warm (Mautz 1985). Differences in body size, locomotion style, and lower critical temperatures between mule deer and white-tailed deer may influence their overwinter survival differently. Additionally, winter influences age classes differently; juvenile survival is typically lower than adult survival during winter (Nelson and Mech 1986, Bishop et al. 2005).

The second hypothesized environmental condition affecting survival is nutrient availability. Experiments have shown that nutrition is limiting in the winter and supplemental feed can increase both adult survival and neonatal survival the following year (Bishop et al. 2009, Jackson et al. 2021). Furthermore, nutrient availability in the fall can affect body condition and therefore overwinter survival (Hurley et al. 2014). Because of the impact of nutrition on survival, deer may follow the “green wave” throughout the year to track plants at their peak nutritional quality and quantity (Merkle et al. 2016).

Finally, drought conditions may decrease survival via two mechanisms. First, plant primary productivity decreases during drought, which leads to reduced quantity and quality of nutritional resources for deer (Lashley and Harper 2012, Jackson et al. 2021). Second, drought conditions are associated with outbreaks of hemorrhagic disease, which can reduce survival in episodic pulses (Christensen et al. 2020). These two factors may affect mule deer and white-tailed deer differently. First, mule deer may be more adapted to subsisting on lower-quality forage than white-tailed deer (Lashley et al. 2015). Second, hemorrhagic disease may decrease survival of white-tailed deer much more dramatically than mule deer (Hoff et al. 1973).

Survival models (e.g., known fate, Cormack-Jolly-Seber, Cox proportional hazards, etc.) can be used to relate environmental variables to survival probability and therefore establish a direct link between habitat and a meaningful metric of population performance and trajectory. However, sample size is a limiting factor making this connection. To understand the survival process of long-lived species, long-term datasets are required to capture the range of conditions an individual experiences over its lifetime. Furthermore, for habitat generalists that may have a large amount of inter-individual variation, the datasets must include large numbers of individuals. Deer, which are both long-lived species and habitat generalists, are difficult and expensive to capture and monitor over long timeframes, so sufficient datasets are rare.

Using a long-term dataset with thousands of individuals, our goal was to understand the environmental conditions that affect survival of mule deer and white-tailed deer in their sympatric range. Due to technological advances over recent years, long-term datasets like ours often include different types of data, particularly telemetry data from very high frequency (VHF) collars and global positioning system (GPS) collars. To complete a survival analysis with both data types, we applied a ragged telemetry model originally developed to estimate avian nest survival. This model allowed us to integrate the two data types and handle the uncertainty inherent to the different types of data. Through this modeling approach, we explored our three hypotheses to explain and predict survival of different ages and sexes of both species at the population level. We determined the effect of each hypothesized environmental factor on monthly survival of males and females of two age classes across 12 years and 10 populations of mule deer and white-tailed deer.

Methods

Study area

Our study area was the state of South Dakota, USA (42°28'14"– 45°56'43" N, 96°25'26"–104°2'44" W). The state was divided into eleven Data Analysis Units (DAUs), which were defined by homogeneous physiographic and climatic features and were used by South Dakota Department of Game, Fish, and Parks (SDGFP) to designate distinct deer populations (Figure 2.1; South Dakota Department of Game, Fish, and Parks 2017).

The three major physiographic regions in South Dakota are West River (west of the Missouri River), East River (east of the Missouri River), and the Black Hills (in the western part of the state). Aside from the Black Hills, which are forested and higher elevation, South Dakota is considered mixed-grass prairie in the northern Great Plains. Elevation ranges from 294 m at Big Stone Lake in the northeast to 2,207 m at Black Elk Peak in the Black Hills. Aside from the Black Hills, which are colder and wetter than the surrounding area, there is a distinct temperature gradient from north (colder) to south (warmer) and precipitation gradient from west (drier) to east (wetter; Figure 2.2). The 30-year mean daily temperature ranged from around 4°C in the north to 10°C in the south, and annual precipitation over the same period ranged from around 38 cm in the west to 71 cm in the east (Fick and Hijmans 2017). Ungulate species in the state in addition to mule deer and white-tailed deer include pronghorn (*Antilocapra americana*) and elk (*Cervus canadensis*). Predator species include mountain lions (*Puma concolor*), coyotes (*Canis latrans*), and bobcats (*Lynx rufus*).

Capture and collaring

From 2009 – 2021, we captured and collared 2,045 mule deer and 3,358 white-tailed deer in 10 of our 11 DAUs. We captured males and females of two age classes: adult (>1 yr) and juvenile (<1 yr). We captured adults in the winter (599 mule deer and 1,162 white-tailed deer), and we captured some juveniles in the spring as neonates (753 mule deer and 1,007 white-tailed deer) and some juveniles in the winter at approximately 6 months of age (693 mule deer and 1,189 white-tailed deer). We primarily used helicopter net-gunning to capture adults and juveniles in winter, and we supplemented winter captures in some DAUs with Clover traps (Clover 1956). For spring capture of juveniles (2013 – 2018), we used a combination of methods to locate neonates, including vaginal implant transmitters (VITs) placed in adult females, grid searching, and driving transects and observing adult female behavior indicating post-partum condition.

We followed the American Society of Mammalogists' guidelines for animal capture and handling (Sikes et al. 2016), and our protocols in 2019 – 2021 were approved by University of Montana Institutional Animal Care and Use Committee (064-18PLWB-121418).

In the earlier years of our study (2009 – 2019), we outfitted each deer with a very high frequency (VHF) collar, and in later years (2019 – 2021) we used global positioning system (GPS) collars. The 4,713 individuals in the earlier years received VHF collars from Advanced Telemetry Systems (Isanti, Minnesota, USA). In the later years, 135 deer received GPS collars from Vectronic Aerospace GmbH (Berlin, Germany) that used the Iridium satellite system and took positions every 5 hours. The other 555 deer with GPS collars received collars from Telonics, Inc. (Mesa, Arizona, USA) that used the

GlobalStar satellite system and took positions every 5 hr (*n* = 81), 11 hr (*n* = 279), or 13 hr (*n* = 195). Juveniles captured in the spring all received expandable collars (all VHF, 68 g). Juvenile and adult female deer captured in the winter received non-expandable collars (VHF 160 g; GPS 495 – 560 g); we padded these collars with temporary foam before deploying on juvenile females to fit their smaller necks and allow for growth. On male deer captured in winter, we deployed expandable collars (VHF 160 g; GPS 270 – 365 g), and we used temporary foam to allow for growth and neck expansion during the rut.

Survival monitoring

From 2009 to 2021, we performed monthly telemetry flights to monitor the status (alive or dead) of VHF collars. Collars emitting mortality signals were pinpointed from the air. In the following days, an observer would investigate whether the signal was from a true mortality event (evidence included blood, bones, and hair) or a broken or slipped collar. When GPS collars sent mortality messages via satellite, an observer located the collar within several days and investigated the site for signs of mortality using the same protocol as for investigating VHF mortalities. Once we collected a collar, we backdated mortality to the date the mortality signal was first heard (VHF) or transmitted (GPS).

Environmental variables

To determine the effect of environmental factors on deer survival at the population level, we collected four covariates to represent our three hypotheses: drought, winter severity and nutrient availability. We aggregated data to monthly values for each DAU using Google Earth Engine (Gorelick et al. 2017). For drought, we used the Palmer Drought

Severity Index (PDSI) from the 4-km daily Gridded Surface Meteorological (GRIDMET) dataset (Palmer 1965, Abatzoglou 2013). We calculated a median monthly value from the daily dataset and then calculated the median value of these to aggregate the 4 km cells to each DAU. PDSI values less than 0 indicated drier conditions and values greater than 0 indicated wetter conditions (Palmer 1965). To quantify winter severity, we calculated two variables: percent snow cover and the number of cold days below the lower critical thermal temperature of deer. We quantified percent snow cover from the daily 500 m resolution MODIS dataset (Hall and Riggs 2016). We calculated the mean value per month and the mean monthly value per DAU to aggregate to our desired spatiotemporal scale. We calculated harsh cold at the DAU level as the number of days per month with a nighttime low below -10°C, based on the lower critical temperature for white-tailed deer (Bunnell et al. 1986). We aggregated the 1km MODIS dataset (Wan et al. 2021) to the DAU by taking the maximum value of the pixels in that DAU. Finally, we represented nutrient availability throughout the year using the normalized difference vegetation index (NDVI; Didan 2021). We aggregated the 16-day dataset to month by taking the median value and then aggregated to DAU by taking the median value of 1km pixels.

Analysis

We used a ragged telemetry model to estimate monthly survival of deer in our study area. This model was developed to measure avian nest survival when the fledge date or nest failure date is unknown (Royle and Dorazio 2008). This same model applies well to telemetry data from VHF or GPS collars in which a collared individual’s fate can be observed but the exact mortality date is not always known (Royle and Dorazio 2008). For example, if a monthly flight cannot be performed for some reason, animals recorded dead during the following month's flight could have died in either of two months. For any missing observations due to a failure to locate a collar (e.g., no flight performed or the animal left the study area), the model integrates over all possible encounter histories that could have occurred, thereby eliminating the need to record the exact interval of death. We extended this idea to estimate the survival probability of individuals whose fates were not observable due to collar failures. If a collar failure occurred, we used the model to integrate over all possible alive/dead encounter histories from the last time the individual was known to be alive until the end of the study. This allowed us to handle individuals with unknown fates without having to right-censor them from our sample. Additionally, the ragged telemetry model conditions survival probability on capture, so it allowed staggered entry without the need for left-censoring individuals. This was particularly useful for our juvenile age class because approximately half of our juveniles entered the study in spring and half entered in winter.

We designated mortalities that occurred within 14 days of capture as capture-related, and we excluded these individuals from the survival analysis (Chalmers and Barrett 1982). We right-censored individuals that died from hunter harvest, so survival rates were interpreted as the probability of survival in the absence of hunting. For individuals whose collars fell off, lost battery power, or failed for any other reason, we allowed the model to integrate over all possible fates for the individual from the time of the last known alive to the end of the study.

We estimated survival probability independently for each species, age class, sex, and year. We used uninformative priors for our beta coefficients (Normal distribution with mean 0 and standard deviation 1.7). We used a Normal(1.5, 1) distribution as a weakly informative prior for baseline survival probability in the absence of covariate effects. After the logit transformation, this prior was weighted toward higher values of monthly survival (i.e., greater than 0.6) because monthly survival is high for long-lived ungulates (Forrester and Wittmer 2013).

Using estimated monthly survival, we derived annual survival for the biological year, which we defined as June 1 – May 30 each year. The first capture event in most DAUs occurred in winter – partially through our defined biological year – therefore the first derived “annual” estimate for that DAU referred to survival from capture through May 30 of that year. For example, in DAU 10, white-tailed deer were first captured in January 2009, so the reported “annual” survival for year 1 was actually survival from January until May 30. Because we used only a partial year, estimated annual survival in the first year for each DAU was higher than true annual survival.

Because we estimated annual survival independently for each DAU, we were able to compare survival across time and space. We summarized survival for each species, sex, and age class from all years and DAUs to capture the spatiotemporal process variance in mean annual survival across deer populations. When comparing annual survival across populations, we removed any “annual” estimates derived from partial years.

We used an information-theoretic approach to select variables to test our hypotheses. Three of our covariates (cold days, percent snow cover, and NDVI) were highly correlated (r^2>0.7; Table 2.1), so we selected only one of these to use in the full model. To select the covariate, we first defined and fit four models, each containing one environmental covariate: snow cover, cold days, NDVI, and PDSI (Figure S2.1 in Appendix 2.1). The deviance information criterion (DIC) supported NDVI as the top-ranked model (Table 2.2). Using NDVI to represent all three correlated covariates, we then created a single model with two covariates: NDVI and PDSI, which had low correlation to the other three variables.

For each of the four initial models and our full model, we allowed the effects of the environmental covariates to vary by species, sex, and age class, so we could compare the differential impact of each covariate on each of these groups. Environmental covariates were centered and scaled, to aid in comparison of effect size. We ran the models in JAGS version 4.3.1 (Plummer 2003) using R version 4.1.3 (R Core Team 2022) and the R2jags package (Su and Yajima 2021). We ran 3 chains for 30,000 iterations each and discarded the first 10,000 iterations as burn-in. We checked for chain convergence visually using trace plots and by R-hat values < 1.1 (Gelman and Rubin 1992).

Results

Survival

Out of 5,086 deer used in our analysis, we observed 2,636 deaths (52%) over our study (Table 2.3). Our monthly monitoring of VHF collars did not allow us to collect cause-specific mortality, but we investigated collar sites for clues and classified mortality to the best of our ability. Therefore, the largest category of mortalities was natural or unknown. This was followed by hunter harvest and vehicle collision (Table 2.3). Forty-two percent of the deer (n = 2,159) outlived their collars because the collar malfunctioned, reached the end of its battery life, or fell off prematurely.

We estimated annual survival for each DAU, species, age class, sex, and year (Table S2.1 in Appendix 2.1). Across all our deer populations and years, we found that mule deer adult female survival (mean = 0.86, SD = 0.04) was the least variable of all the vital rates (Table 2.4). Mule deer juvenile survival was the lowest of any survival rate (female 0.37; male 0.31). For both species, juvenile survival was lower and more variable than adult female survival of that species.

Landscape inventory

Over our 12-year study, we measured spatio-temporal variation in the four environmental variables we collected to represent our hypotheses (Figure 2.3). First, to represent winter harshness, we collected the number of cold days per month (days with a nighttime low below -10° C) and the monthly percent of snow cover in each DAU. The number of cold days varied throughout the year, from 0 in summer months to 24 days in the coldest winters. Monthly cold days was relatively consistent between years and between DAUs (Figure 2.3). The second winter variable, snow cover, also varied throughout the year, as expected, from 0% in summer months to 79% in the snowiest winter. Similar to monthly cold days, snow cover was relatively consistent across DAUs and across time, with the exception of 2012, which had very little snow compared to other years (Figure 2.3).

Monthly NDVI values during our study ranged from -0.04 to 0.85. We recorded high temporal variation in NDVI throughout the year, with lowest values in the winter months and highest values in the summer months (Figure 2.3). Values of NDVI below

0.1 (including negative values) represented barren ground or snow whereas high values from approximately 0.6 to 0.9 corresponded to high vegetative greenness, such as crops during peak growth (Remote Sensing Phenology 2018). There was some variation in NDVI between DAUs, but yearly cycles were relatively consistent, with the exception of 2012, which showed higher-than-average NDVI values during winter (likely due to less snow cover) and lower-than-average NDVI values the following summer.

Our drought severity index, PDSI, varied less within a year than the other three environmental variables but more between years (Figure 2.3). It also showed more variability between DAUs than the other environmental variables. We recorded values from -5.6 in 2012 to 9.17 in 2019. PDSI values between -1 and 1 are considered “normal” (neither drought nor wet conditions) and negative numbers indicate drier conditions while positive numbers indicate wetter conditions (Abatzoglou 2013). Values below -5 are considered extreme drought and values above 5 are extremely wet conditions.

Environmental effects

We considered covariate effects to be significant if at least 95% of the posterior distribution was on the same side of 0 as the mean. We found consistent evidence that higher NDVI was associated with decreased survival in juveniles of both species and sexes (Figure 2.4). The standard deviation was an order of magnitude smaller than the mean and approximately 100% of the posterior distribution was on the same side of 0 as the mean, indicating evidence of an effect. For adults, the effect of NDVI on survival varied by species; there was no measurable effect on survival of mule deer adult females (-0.06, SD 0.06) or males (-0.03, SD 0.14), but higher NDVI was associated with increased survival of white-tailed deer adult females (0.15, SD 0.04) and males (0.56, SD 0.07).

Overall, drought (represented by PDSI) had little effect on survival (Figure 2.4). The positive relationship of PDSI with survival of white-tailed deer female juveniles (0.22, SD 0.12) indicated that wetter conditions increased survival and drier conditions decreased survival for this group. However, drought had the opposite effect on mule deer female juveniles (-0.26, SD 0.13) and white-tailed deer adult males (-0.22, SD 0.13). For all three of these groups with a detected effect, there was a large standard error relative to the mean and the 95% Bayesian Credible Interval (BCI) overlapped 0, so the effects were not strong. Furthermore, we found no effect of PDSI on male juveniles of either species, no effect on mule deer adults, and no effect on white-tailed deer adult females.

Discussion

The ragged telemetry survival model was a flexible approach to estimating survival that allowed us to combine a VHF telemetry dataset with finer-scale GPS collar data. It integrated over all possible fates when an individual’s exact fate date was unobservable, which was a greater source of uncertainty in the VHF data than GPS data and would have been an obstacle in combining the two datasets in a purely known fate model. Despite monthly effort, some VHF collars were not located from the air for several months due to a variety of reasons, including individuals moving long distances or collars malfunctioning. Therefore, mortalities were sometimes found months after the individual was last known to be alive, creating uncertainty in the death date. Furthermore, the ragged telemetry survival model approach also allowed us to integrate over all possible fates for individuals that outlived their collars (nearly half of all individuals) without needing to remove them from the sample. This feature allows for continual updating of the model if new mortality information comes in (e.g., the collar is returned by a hunter or found on a road-killed animal).

Consistent with known demographic patterns in ungulates, we found that adult survival was higher and less variable than juvenile survival in both species (Gaillard et al. 2000). The greatest number of effects and largest effect sizes we found from the environmental covariates were among juveniles, which was likely because juvenile survival was more variable than adult survival (Figure 2.4). Our estimate of mean mule deer adult female survival (0.856) matched the range-wide mean of mule deer adult survival (0.84, 95% CI 0.76-0.94; Forrester and Wittmer 2013). Mule deer juvenile survival (females 0.37; males 0.31) also fell in the range-wide mean (0.29, 95% CI: 0.19 – 0.39) and may have been on the upper end (Forrester and Wittmer 2013). There is a large amount of variation in white-tailed deer survival between studies (adult females 0.44 – 0.93, adult males 0.27 – 0.97), and our estimates (adult females 0.82; adult males 0.72) also fell within these bounds (DeYoung 2011). These values showed that mean adult survival was comparable between mule deer and white-tailed deer in South Dakota over our study period. However, juvenile survival of white-tailed deer was much higher than mule deer, with approximately the same amount of variability. Low mule deer recruitment of fawns may be a critical factor for conserving mule deer populations, and our results could indicate a competitive advantage of white-tailed deer over mule deer in the areas where they coexist (Carpenter 1997).

With our extensive, long-term dataset, we aimed to understand the environmental variables affecting mule deer and white-tailed deer survival at the population level, and we found little support for any of our hypotheses. We used a single variable, NDVI, to test our first two hypotheses: (1) harsh winters decrease survival and (2) nutrient availability increases survival. The limited support for these hypotheses was the positive effect of NDVI on white-tailed deer adults, which indicated that higher nutrient availability (and by extension to the correlated variables, lower snow cover and fewer cold days) increased monthly survival, as predicted. However, higher values of NDVI *decreased* survival in juveniles of both species and had no effect on mule deer adults. This suggested that lower nutrient availability and harsher winters increased survival of juveniles, which was unexpected. Because deer are concentrate selectors, NDVI may not always correlate with higher nutrient availability, as plant parts that are not eaten can contribute to the overall greenness score (Zimmerman et al. 2006, Lashley et al. 2014). Additionally, our metrics of winter severity showed little variation between years, with only one particularly mild winter recorded and no extremely harsh winters. This indicated that within the range of conditions in typical winters, there was little support for winter harshness decreasing survival.

Our third hypothesis – drought conditions would decrease monthly survival through either decreased access to quality forage or increased risk of disease transmission – was also largely unsupported. Although we found that drought had a negative effect on white-tailed deer juvenile female survival as predicted, the effect size was small and uncertain. For every other species, age class, and sex, drought had no effect on survival or the opposite effect of what was predicted. These results did not follow any biologically meaningful patterns that could describe or predict survival at the population level. Over our 12-year study, we recorded a wide range of drought conditions, from extreme drought to extreme wet, yet there was no measurable effect at the population level. Mule deer and white-tailed deer are habitat generalists that can persist in a wide range of conditions; their physiological and behavioral adaptations appeared to allow individuals to survive at a similar rate across highly variable conditions. It also may be possible that sustained drought conditions over a longer time would be necessary to cause a decrease in survival at the population level.

Although our results showed little support for our hypotheses and highlighted some counterintuitive patterns, they are in keeping with the inconsistent results found in the literature. For example, snow depth or winter precipitation are commonly used environmental variables in habitat selection and demographic studies, and they have been associated with decreased survival of white-tailed deer (DelGiudice et al. 2002), mule deer adults (Jackson et al. 2021), and mule deer juveniles (Forrester and Wittmer 2013, Hurley et al. 2014). However, they have also been shown to have the opposite or no effect on mule deer adults (Forrester and Wittmer 2013, Schuyler et al. 2019) and unlikely to have an effect on mule deer juveniles (Bergman et al. 2014). Given the contradictory evidence across time and space, it is likely that snow is only limiting in severe winters, so it does not have a consistent effect on survival across years (Jackson et al. 2021). The same may be true about our measures of forage, winter severity, and drought. Experiments have shown that deer survival is linked to nutritional condition (Bishop et al. 2009), but inter-individual variability within a population may be large enough to drown out any effects of the environment when conditions are within normal bounds. These results suggest further support for the conclusion that environmental variables cannot predict an individual's probability of survival better than more direct measures such as body mass (Bishop et al. 2005).

For long-lived species like deer, the effects of nutritional stress and cold exposure likely function on a longer timeframe than we were able to capture in our study. For example, summer and fall nutrient availability affect an individual's body condition and therefore its resilience to winter (Rowland et al. 2018). Therefore, the limiting factors for survival may occur months before the winter conditions that are proximally responsible for mortality. However, the ragged telemetry model we used was formulated to link survival to environmental conditions occurring at the time of observation, not months before. To use this and other survival models to quantify the effect of variables that have longer-term effects, researchers must use lag effects (e.g., Hurley et al. 2014, Jackson et al. 2021). However, lag effects must be assigned specific time delays (e.g., a lag of one month, two months, etc.), and in the absence of experimental data, the scale can be very hard to define and may be arbitrary. Thus, there is a need for modeling approaches that improve our ability to capture long-term processes effectively. In the next chapter, we introduce a new model to address these limitations of current methodologies.

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Tables

Table 2.1. Collinearity of environmental variables (r^2).

	Cold days	PDSI	NDVI	Snow cover
Cold days	1	-	-	-
PDSI	0.009	1	-	-
NDVI	-0.800	0.030	1	-
Snow cover	0.800	0.116	-0.740	1

Table 2.2. Model selection between four hypothesized drivers of survival probability using deviance information criterion (DIC).

Model	DIC	ΔDIC
NDVI	23030.9	0.0
Cold days	23229.8	198.9
Snow cover	23416.7	385.8
PDSI	23771.8	740.9

Table 2.3. Causes of observed mortalities. We did not aim to get cause-specific mortality, so the greatest number of mortalities were categorized as Natural or Unknown.

Fate	n
Alive	291
Capture-related	317
Hunter harvest	340
Collar failure	2,159
Natural or unknown	2,167
Vehicle collision	129
Total	**5,403**

Table 2.4. Annual survival in the absence of harvest for juvenile (<1 yr) and adult (>1yr) mule deer and white-tailed deer across 10 populations and 12 years.

Species	Age	Sex	Mean	SD	n[1]
Mule Deer	adult	female	0.856	0.043	49
Mule Deer	adult	male	0.743	0.062	36
Mule Deer	juvenile	female	0.374	0.135	16
Mule Deer	juvenile	male	0.314	0.133	16
White-tailed Deer	adult	female	0.822	0.082	62
White-tailed Deer	adult	male	0.724	0.062	48
White-tailed Deer	juvenile	female	0.493	0.133	20
White-tailed Deer	juvenile	male	0.452	0.117	20

[1] sample size = number of DAU-specific annual survival estimates

Figures

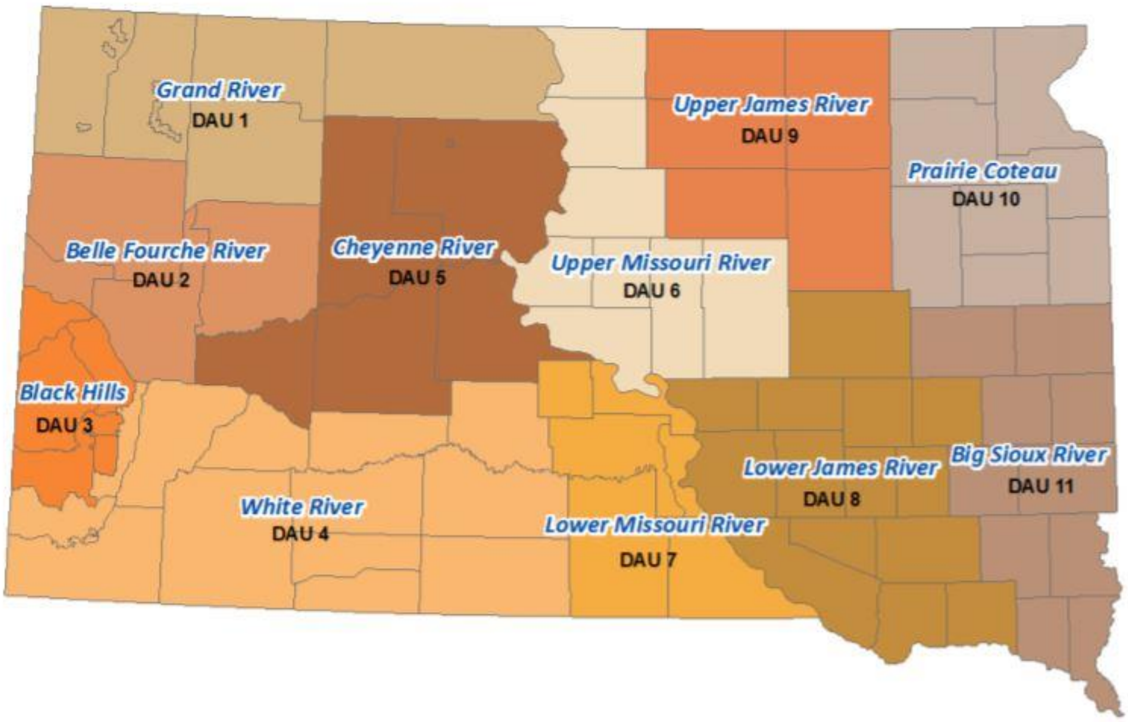

Figure 2.1. Data analysis units (DAUs) of South Dakota.

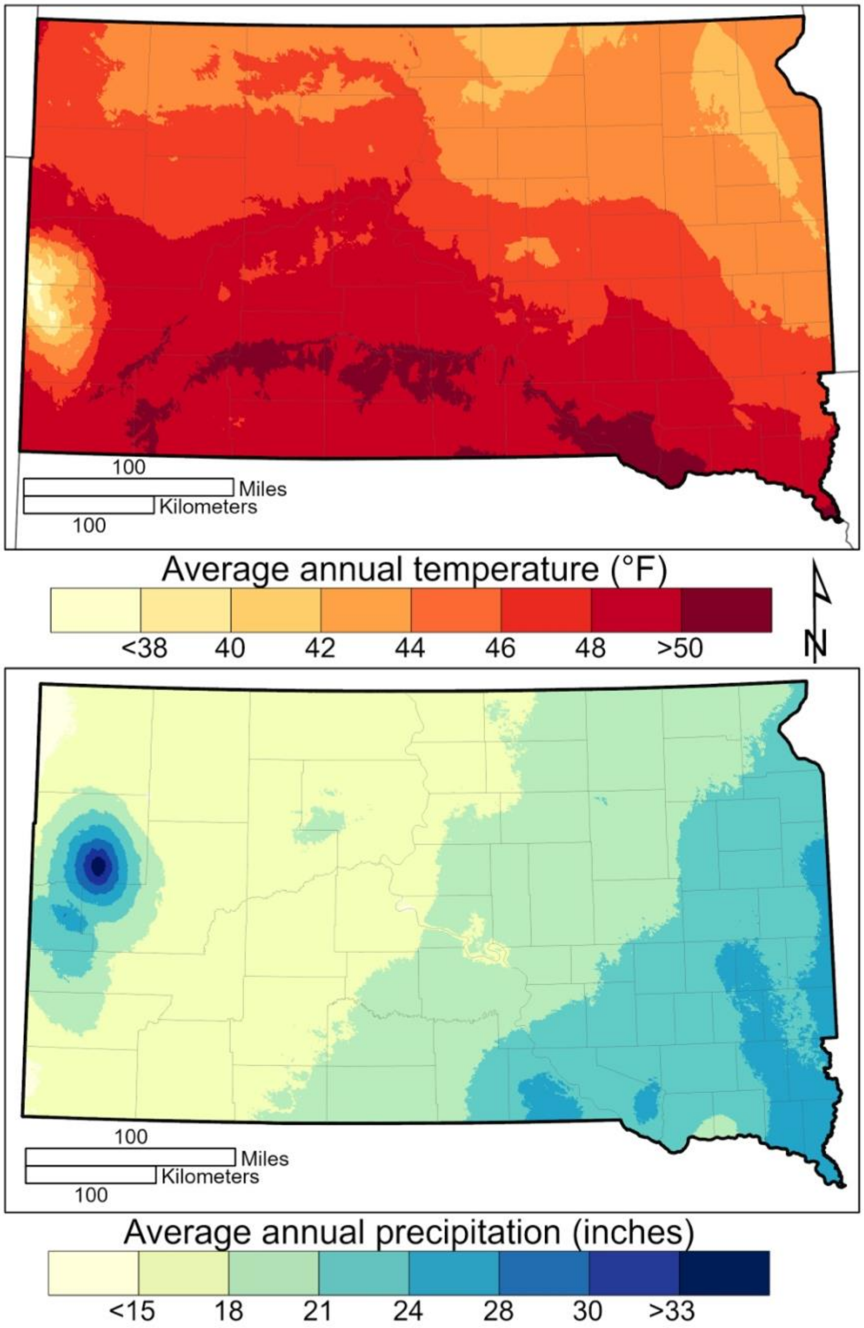

Figure 2.2. General variability of temperature and precipitation in South Dakota, USA, 1970–2000. Map by Samantha Nichols, data from Fick and Hijmans (2017).

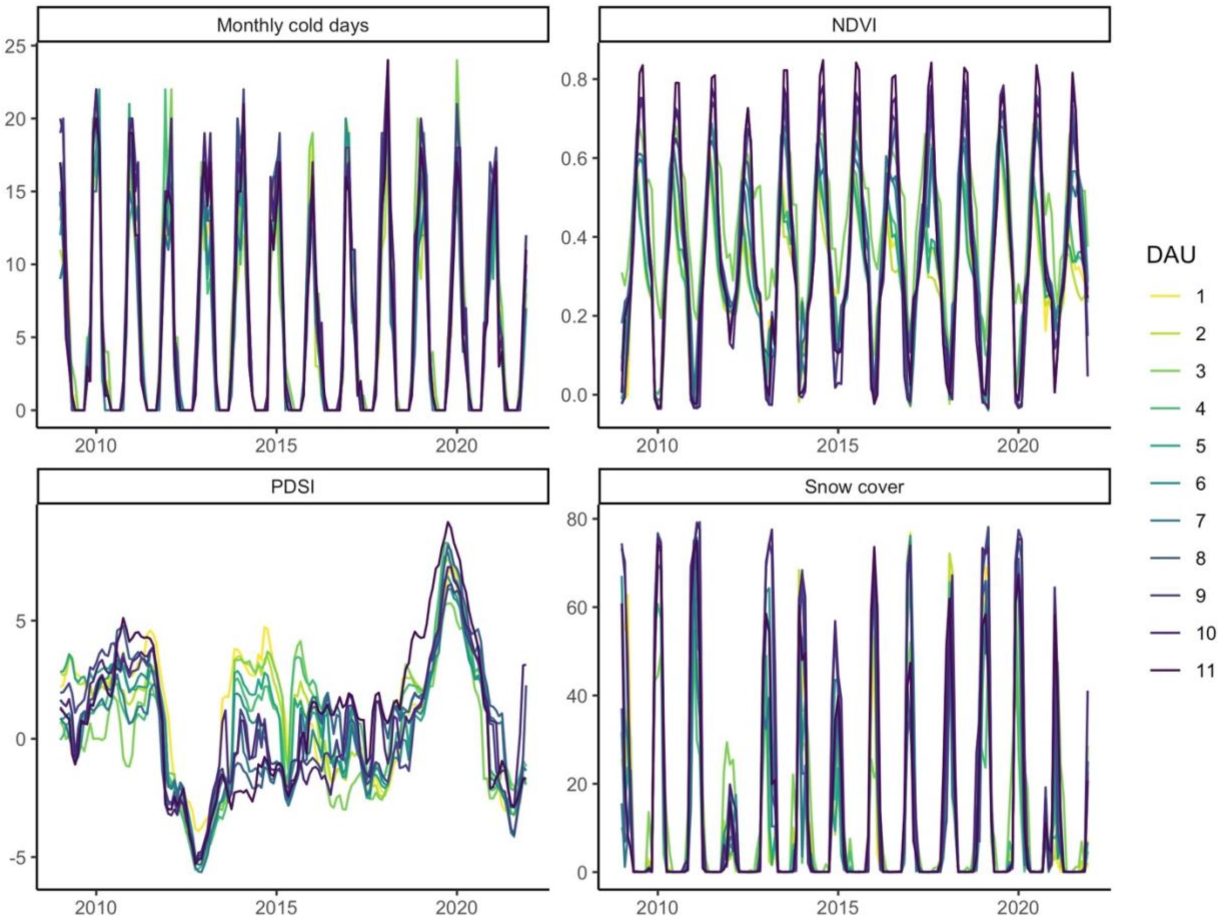

Figure 2.3. Monthly values of environmental variables recorded for each Data Analysis Unit (DAU) from January 2009 – December 2021.

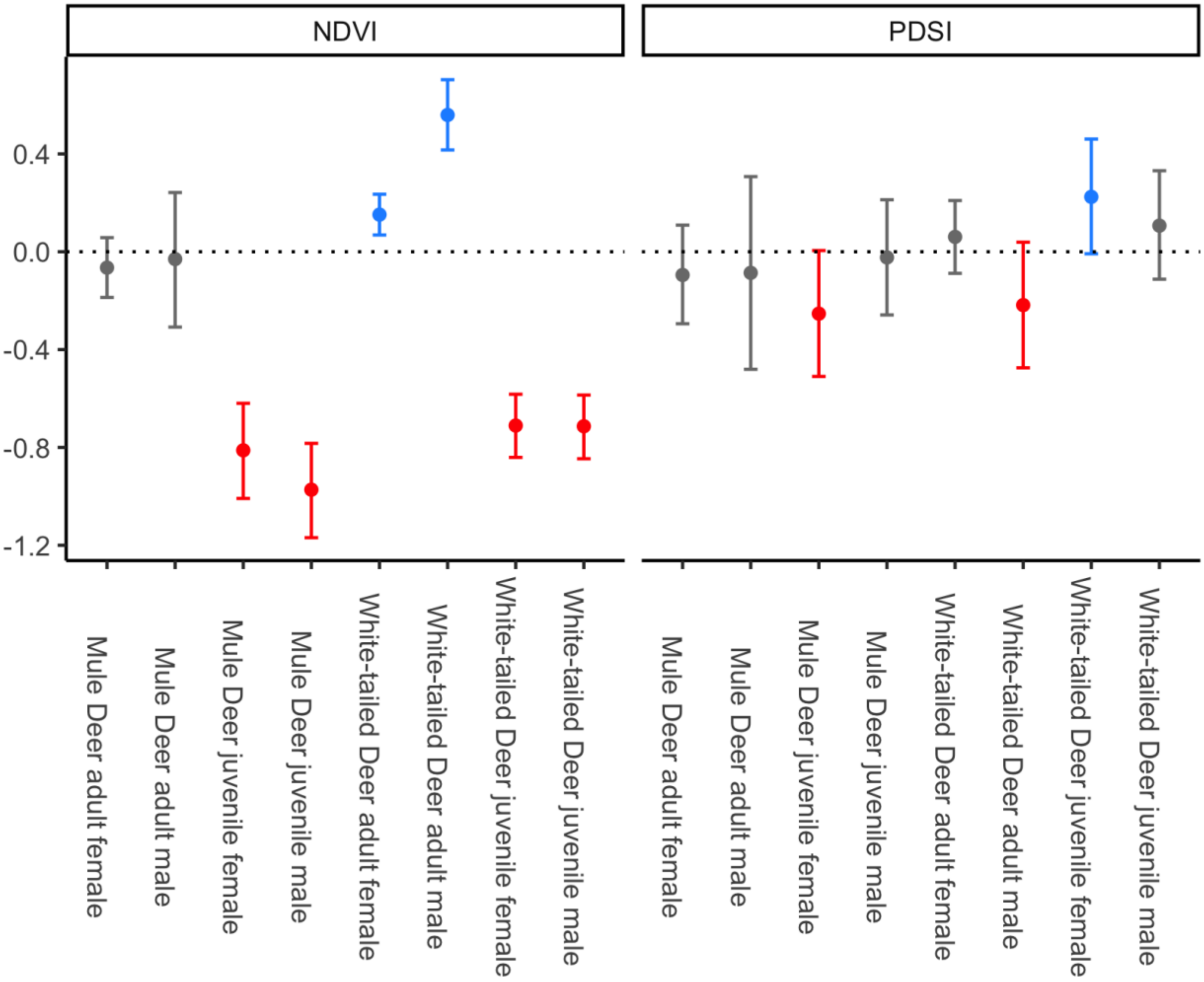

Figure 2.4. Estimated effects of normalized difference vegetation index (NDVI) and Palmer's drought severity index (PDSI) on monthly survival probability by species, age class, and sex, including 95% Bayesian credible interval.

Appendix 2.1

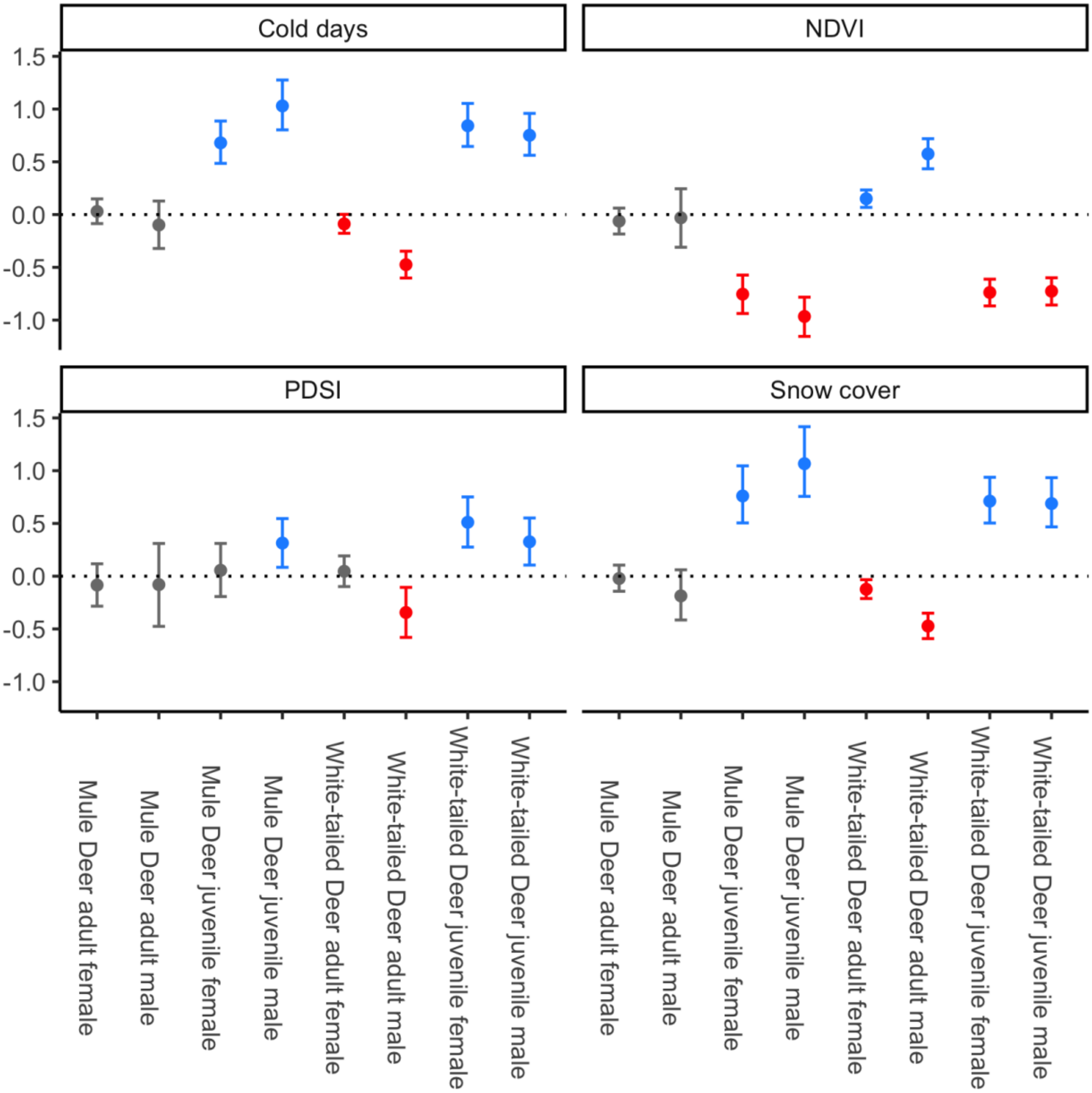

Figure S2.1. Estimated effects of number of monthly cold days, normalized difference vegetation index (NDVI), Palmer's drough severity index (PDSI), and percent snow cover on survival of mule deer and white-tailed deer adults (>1 yr) and juveniles (<1 yr). Models were fit separately.

Table S2.1. Estimates of annual survival for each DAU, species, age class, sex, and year, given a minimum of 10 individuals were monitored.

parameter	species	age	sex	bioyear	yr	DAU	mean	sd	n
partial year	Mule Deer	adult	female	2009	2	2	0.519	0.083	39
partial year	Mule Deer	adult	female	2009	2	7	0.520	0.083	48
annual	Mule Deer	adult	female	2010	3	2	0.721	0.082	44
annual	Mule Deer	adult	female	2010	3	7	0.719	0.082	53
annual	Mule Deer	adult	female	2011	4	2	0.878	0.051	54
annual	Mule Deer	adult	female	2011	4	7	0.876	0.052	40
annual	Mule Deer	adult	female	2012	5	2	0.875	0.046	51
annual	Mule Deer	adult	female	2012	5	7	0.873	0.047	36
annual	Mule Deer	adult	female	2013	6	2	0.920	0.035	44
annual	Mule Deer	adult	female	2013	6	7	0.924	0.034	23
annual	Mule Deer	adult	female	2014	7	2	0.904	0.030	50
partial year	Mule Deer	adult	female	2014	7	3	0.967	0.011	38
annual	Mule Deer	adult	female	2014	7	4	0.907	0.029	52
partial year	Mule Deer	adult	female	2014	7	6	0.971	0.010	49
annual	Mule Deer	adult	female	2014	7	7	0.913	0.028	31
annual	Mule Deer	adult	female	2015	8	2	0.909	0.019	54
annual	Mule Deer	adult	female	2015	8	3	0.901	0.021	109
annual	Mule Deer	adult	female	2015	8	4	0.905	0.020	111
annual	Mule Deer	adult	female	2015	8	6	0.912	0.019	109
annual	Mule Deer	adult	female	2015	8	7	0.910	0.019	37
annual	Mule Deer	adult	female	2016	9	2	0.851	0.018	52
annual	Mule Deer	adult	female	2016	9	3	0.847	0.020	122
annual	Mule Deer	adult	female	2016	9	4	0.844	0.019	141
annual	Mule Deer	adult	female	2016	9	6	0.843	0.019	126
annual	Mule Deer	adult	female	2016	9	7	0.838	0.020	37
annual	Mule Deer	adult	female	2017	10	2	0.890	0.017	44
annual	Mule Deer	adult	female	2017	10	3	0.884	0.017	132
annual	Mule Deer	adult	female	2017	10	4	0.886	0.017	157
annual	Mule Deer	adult	female	2017	10	6	0.888	0.016	142
annual	Mule Deer	adult	female	2017	10	7	0.881	0.018	37
partial year	Mule Deer	adult	female	2018	11	1	0.942	0.008	102
annual	Mule Deer	adult	female	2018	11	2	0.860	0.017	36
annual	Mule Deer	adult	female	2018	11	3	0.854	0.018	122
annual	Mule Deer	adult	female	2018	11	4	0.859	0.017	201

annual	Mule Deer	adult	female	2018	11	6	0.866	0.017	198
annual	Mule Deer	adult	female	2018	11	7	0.860	0.017	37
annual	Mule Deer	adult	female	2019	12	1	0.830	0.019	116
annual	Mule Deer	adult	female	2019	12	2	0.828	0.019	36
annual	Mule Deer	adult	female	2019	12	3	0.829	0.020	120
annual	Mule Deer	adult	female	2019	12	4	0.825	0.020	175
annual	Mule Deer	adult	female	2019	12	6	0.833	0.019	177
annual	Mule Deer	adult	female	2019	12	7	0.826	0.020	37
annual	Mule Deer	adult	female	2020	13	1	0.842	0.021	133
annual	Mule Deer	adult	female	2020	13	2	0.842	0.021	36
annual	Mule Deer	adult	female	2020	13	3	0.837	0.022	101
annual	Mule Deer	adult	female	2020	13	4	0.839	0.021	161
annual	Mule Deer	adult	female	2020	13	6	0.838	0.021	153
annual	Mule Deer	adult	female	2020	13	7	0.829	0.024	37
annual	Mule Deer	adult	female	2021	14	1	0.825	0.025	154
annual	Mule Deer	adult	female	2021	14	2	0.828	0.025	36
annual	Mule Deer	adult	female	2021	14	3	0.815	0.028	92
annual	Mule Deer	adult	female	2021	14	4	0.822	0.026	150
annual	Mule Deer	adult	female	2021	14	6	0.822	0.026	134
annual	Mule Deer	adult	female	2021	14	7	0.819	0.026	37
annual	Mule Deer	juvenile	female	2013	6	2	0.459	0.081	18
annual	Mule Deer	juvenile	female	2013	6	7	0.346	0.080	19
annual	Mule Deer	juvenile	female	2014	7	2	0.305	0.086	17
annual	Mule Deer	juvenile	female	2014	7	7	0.346	0.088	15
annual	Mule Deer	juvenile	female	2015	8	3	0.408	0.066	33
annual	Mule Deer	juvenile	female	2015	8	4	0.596	0.056	38
annual	Mule Deer	juvenile	female	2015	8	6	0.628	0.061	36
annual	Mule Deer	juvenile	female	2016	9	3	0.316	0.052	53
annual	Mule Deer	juvenile	female	2016	9	4	0.468	0.048	57
annual	Mule Deer	juvenile	female	2016	9	6	0.419	0.048	52
annual	Mule Deer	juvenile	female	2017	10	3	0.254	0.041	39
annual	Mule Deer	juvenile	female	2017	10	4	0.445	0.042	82
annual	Mule Deer	juvenile	female	2017	10	6	0.411	0.042	84
annual	Mule Deer	juvenile	female	2018	11	3	0.283	0.073	34
annual	Mule Deer	juvenile	female	2019	12	1	0.097	0.048	55
annual	Mule Deer	juvenile	female	2020	13	1	0.210	0.095	52
annual	Mule Deer	adult	male	2014	7	2	0.688	0.137	14
annual	Mule Deer	adult	male	2014	7	7	0.709	0.138	12
annual	Mule Deer	adult	male	2015	8	2	0.803	0.090	27

annual	Mule Deer	adult	male	2015	8	7	0.804	0.090	15
annual	Mule Deer	adult	male	2016	9	2	0.823	0.053	27
annual	Mule Deer	adult	male	2016	9	3	0.822	0.055	20
annual	Mule Deer	adult	male	2016	9	4	0.817	0.054	33
annual	Mule Deer	adult	male	2016	9	6	0.816	0.054	24
annual	Mule Deer	adult	male	2016	9	7	0.812	0.055	15
annual	Mule Deer	adult	male	2017	10	2	0.806	0.052	26
annual	Mule Deer	adult	male	2017	10	3	0.801	0.052	39
annual	Mule Deer	adult	male	2017	10	4	0.802	0.052	59
annual	Mule Deer	adult	male	2017	10	6	0.805	0.051	63
annual	Mule Deer	adult	male	2017	10	7	0.794	0.056	15
annual	Mule Deer	adult	male	2018	11	2	0.799	0.044	26
annual	Mule Deer	adult	male	2018	11	3	0.796	0.044	52
annual	Mule Deer	adult	male	2018	11	4	0.799	0.043	97
annual	Mule Deer	adult	male	2018	11	6	0.806	0.040	119
annual	Mule Deer	adult	male	2018	11	7	0.801	0.041	15
annual	Mule Deer	adult	male	2019	12	2	0.686	0.081	26
annual	Mule Deer	adult	male	2019	12	3	0.692	0.082	61
annual	Mule Deer	adult	male	2019	12	4	0.681	0.083	91
annual	Mule Deer	adult	male	2019	12	6	0.692	0.081	110
annual	Mule Deer	adult	male	2019	12	7	0.684	0.081	15
annual	Mule Deer	adult	male	2020	13	1	0.681	0.086	24
annual	Mule Deer	adult	male	2020	13	2	0.681	0.086	26
annual	Mule Deer	adult	male	2020	13	3	0.678	0.091	55
annual	Mule Deer	adult	male	2020	13	4	0.678	0.086	88
annual	Mule Deer	adult	male	2020	13	6	0.678	0.087	106
annual	Mule Deer	adult	male	2020	13	7	0.664	0.093	15
annual	Mule Deer	adult	male	2021	14	1	0.692	0.059	55
annual	Mule Deer	adult	male	2021	14	2	0.695	0.059	26
annual	Mule Deer	adult	male	2021	14	3	0.683	0.069	55
annual	Mule Deer	adult	male	2021	14	4	0.688	0.060	88
annual	Mule Deer	adult	male	2021	14	6	0.689	0.061	106
annual	Mule Deer	adult	male	2021	14	7	0.687	0.062	15
annual	Mule Deer	juvenile	male	2013	6	2	0.409	0.081	17
annual	Mule Deer	juvenile	male	2013	6	7	0.199	0.067	23
annual	Mule Deer	juvenile	male	2014	7	2	0.244	0.062	25
annual	Mule Deer	juvenile	male	2014	7	7	0.175	0.058	20
annual	Mule Deer	juvenile	male	2015	8	3	0.248	0.051	35
annual	Mule Deer	juvenile	male	2015	8	4	0.478	0.053	41

annual	Mule Deer	juvenile	male	2015	8	6	0.420	0.061	41
annual	Mule Deer	juvenile	male	2016	9	3	0.209	0.044	44
annual	Mule Deer	juvenile	male	2016	9	4	0.464	0.049	47
annual	Mule Deer	juvenile	male	2016	9	6	0.392	0.048	56
annual	Mule Deer	juvenile	male	2017	10	3	0.255	0.044	40
annual	Mule Deer	juvenile	male	2017	10	4	0.523	0.045	72
annual	Mule Deer	juvenile	male	2017	10	6	0.437	0.045	73
annual	Mule Deer	juvenile	male	2018	11	3	0.268	0.069	35
annual	Mule Deer	juvenile	male	2019	12	1	0.058	0.037	42
annual	Mule Deer	juvenile	male	2020	13	1	0.240	0.093	52
partial year	White-tailed Deer	adult	female	2008	1	10	0.554	0.133	26
partial year	White-tailed Deer	adult	female	2008	1	8	0.649	0.114	25
annual	White-tailed Deer	adult	female	2009	2	10	0.638	0.106	44
annual	White-tailed Deer	adult	female	2009	2	8	0.640	0.105	43
annual	White-tailed Deer	adult	female	2010	3	10	0.794	0.076	37
annual	White-tailed Deer	adult	female	2010	3	8	0.802	0.074	33
annual	White-tailed Deer	adult	female	2011	4	10	0.842	0.062	46
annual	White-tailed Deer	adult	female	2011	4	8	0.845	0.061	25
annual	White-tailed Deer	adult	female	2012	5	10	0.629	0.080	68
annual	White-tailed Deer	adult	female	2012	5	8	0.631	0.080	17
partial year	White-tailed Deer	adult	female	2013	6	1	0.946	0.019	49
annual	White-tailed Deer	adult	female	2013	6	10	0.845	0.048	54
partial year	White-tailed Deer	adult	female	2013	6	11	0.938	0.021	46
annual	White-tailed Deer	adult	female	2013	6	8	0.845	0.048	17
annual	White-tailed Deer	adult	female	2014	7	1	0.918	0.023	49
annual	White-tailed Deer	adult	female	2014	7	10	0.910	0.025	58
annual	White-tailed Deer	adult	female	2014	7	11	0.912	0.024	62
partial year	White-tailed Deer	adult	female	2014	7	3	0.965	0.010	72
annual	White-tailed Deer	adult	female	2014	7	8	0.912	0.025	17
partial year	White-tailed Deer	adult	female	2014	7	9	0.967	0.010	49
annual	White-tailed Deer	adult	female	2015	8	1	0.895	0.019	56
annual	White-tailed Deer	adult	female	2015	8	10	0.892	0.021	68
annual	White-tailed Deer	adult	female	2015	8	11	0.897	0.019	136
annual	White-tailed Deer	adult	female	2015	8	3	0.910	0.017	111
annual	White-tailed Deer	adult	female	2015	8	8	0.898	0.019	17
annual	White-tailed Deer	adult	female	2015	8	9	0.894	0.020	102
annual	White-tailed Deer	adult	female	2016	9	1	0.856	0.018	61
annual	White-tailed Deer	adult	female	2016	9	10	0.864	0.017	65
annual	White-tailed Deer	adult	female	2016	9	11	0.873	0.017	158

annual	White-tailed Deer	adult	female	2016	9	3	0.870	0.018	124
annual	White-tailed Deer	adult	female	2016	9	7	0.868	0.017	22
annual	White-tailed Deer	adult	female	2016	9	8	0.871	0.016	119
annual	White-tailed Deer	adult	female	2016	9	9	0.866	0.017	131
annual	White-tailed Deer	adult	female	2017	10	1	0.870	0.017	51
annual	White-tailed Deer	adult	female	2017	10	10	0.881	0.015	167
annual	White-tailed Deer	adult	female	2017	10	11	0.884	0.015	177
annual	White-tailed Deer	adult	female	2017	10	3	0.884	0.015	126
annual	White-tailed Deer	adult	female	2017	10	7	0.882	0.015	22
annual	White-tailed Deer	adult	female	2017	10	8	0.884	0.015	144
annual	White-tailed Deer	adult	female	2017	10	9	0.877	0.015	169
annual	White-tailed Deer	adult	female	2018	11	1	0.839	0.015	149
annual	White-tailed Deer	adult	female	2018	11	10	0.839	0.015	209
annual	White-tailed Deer	adult	female	2018	11	11	0.852	0.016	233
annual	White-tailed Deer	adult	female	2018	11	3	0.856	0.014	120
annual	White-tailed Deer	adult	female	2018	11	7	0.847	0.014	22
annual	White-tailed Deer	adult	female	2018	11	8	0.847	0.014	188
annual	White-tailed Deer	adult	female	2018	11	9	0.837	0.016	215
annual	White-tailed Deer	adult	female	2019	12	1	0.842	0.015	155
annual	White-tailed Deer	adult	female	2019	12	10	0.840	0.015	217
annual	White-tailed Deer	adult	female	2019	12	11	0.848	0.015	207
annual	White-tailed Deer	adult	female	2019	12	3	0.851	0.015	129
annual	White-tailed Deer	adult	female	2019	12	7	0.845	0.015	22
annual	White-tailed Deer	adult	female	2019	12	8	0.846	0.015	212
annual	White-tailed Deer	adult	female	2019	12	9	0.838	0.016	182
annual	White-tailed Deer	adult	female	2020	13	1	0.794	0.021	211
annual	White-tailed Deer	adult	female	2020	13	10	0.806	0.019	190
annual	White-tailed Deer	adult	female	2020	13	11	0.802	0.020	189
annual	White-tailed Deer	adult	female	2020	13	3	0.813	0.021	109
annual	White-tailed Deer	adult	female	2020	13	7	0.812	0.019	22
annual	White-tailed Deer	adult	female	2020	13	8	0.813	0.019	175
annual	White-tailed Deer	adult	female	2020	13	9	0.804	0.020	172
annual	White-tailed Deer	adult	female	2021	14	1	0.653	0.031	225
annual	White-tailed Deer	adult	female	2021	14	10	0.681	0.037	175
annual	White-tailed Deer	adult	female	2021	14	11	0.673	0.030	189
annual	White-tailed Deer	adult	female	2021	14	3	0.691	0.029	104
annual	White-tailed Deer	adult	female	2021	14	7	0.675	0.030	22
annual	White-tailed Deer	adult	female	2021	14	8	0.674	0.030	147
annual	White-tailed Deer	adult	female	2021	14	9	0.676	0.032	161

annual	White-tailed Deer	juvenile	female	2013	6	10	0.399	0.076	42
annual	White-tailed Deer	juvenile	female	2013	6	11	0.326	0.076	33
annual	White-tailed Deer	juvenile	female	2014	7	1	0.554	0.069	14
annual	White-tailed Deer	juvenile	female	2014	7	10	0.404	0.063	22
annual	White-tailed Deer	juvenile	female	2014	7	11	0.326	0.063	43
annual	White-tailed Deer	juvenile	female	2014	7	7	0.423	0.068	32
annual	White-tailed Deer	juvenile	female	2015	8	1	0.682	0.041	11
annual	White-tailed Deer	juvenile	female	2015	8	11	0.506	0.051	62
annual	White-tailed Deer	juvenile	female	2015	8	3	0.559	0.057	36
annual	White-tailed Deer	juvenile	female	2015	8	7	0.570	0.048	25
annual	White-tailed Deer	juvenile	female	2015	8	9	0.572	0.047	73
annual	White-tailed Deer	juvenile	female	2016	9	11	0.539	0.053	78
annual	White-tailed Deer	juvenile	female	2016	9	3	0.445	0.056	48
partial year	White-tailed Deer	juvenile	female	2016	9	8	0.854	0.020	29
annual	White-tailed Deer	juvenile	female	2016	9	9	0.571	0.044	96
partial year	White-tailed Deer	juvenile	female	2017	10	10	0.865	0.017	53
annual	White-tailed Deer	juvenile	female	2017	10	11	0.393	0.045	78
annual	White-tailed Deer	juvenile	female	2017	10	3	0.334	0.043	47
partial year	White-tailed Deer	juvenile	female	2017	10	8	0.843	0.020	66
annual	White-tailed Deer	juvenile	female	2017	10	9	0.429	0.041	87
partial year	White-tailed Deer	juvenile	female	2018	11	10	0.871	0.020	45
annual	White-tailed Deer	juvenile	female	2018	11	3	0.352	0.054	54
partial year	White-tailed Deer	juvenile	female	2018	11	8	0.837	0.024	56
annual	White-tailed Deer	juvenile	female	2019	12	1	0.642	0.100	65
annual	White-tailed Deer	juvenile	female	2020	13	1	0.827	0.073	58
annual	White-tailed Deer	adult	male	2014	7	10	0.693	0.109	13
annual	White-tailed Deer	adult	male	2014	7	11	0.731	0.099	10
partial year	White-tailed Deer	adult	male	2014	7	3	0.870	0.054	21
partial year	White-tailed Deer	adult	male	2014	7	9	0.917	0.035	48
annual	White-tailed Deer	adult	male	2015	8	1	0.722	0.053	12
annual	White-tailed Deer	adult	male	2015	8	10	0.739	0.053	29
annual	White-tailed Deer	adult	male	2015	8	11	0.695	0.058	22
annual	White-tailed Deer	adult	male	2015	8	3	0.796	0.045	39
annual	White-tailed Deer	adult	male	2015	8	9	0.743	0.051	69
annual	White-tailed Deer	adult	male	2016	9	1	0.699	0.047	29
annual	White-tailed Deer	adult	male	2016	9	10	0.693	0.048	29
annual	White-tailed Deer	adult	male	2016	9	11	0.719	0.047	48
annual	White-tailed Deer	adult	male	2016	9	3	0.826	0.032	95
annual	White-tailed Deer	adult	male	2016	9	7	0.748	0.039	18

annual	White-tailed Deer	adult	male	2016	9	9	0.715	0.044	116
annual	White-tailed Deer	adult	male	2017	10	1	0.616	0.044	29
annual	White-tailed Deer	adult	male	2017	10	10	0.598	0.045	29
annual	White-tailed Deer	adult	male	2017	10	11	0.578	0.052	81
annual	White-tailed Deer	adult	male	2017	10	3	0.713	0.034	145
annual	White-tailed Deer	adult	male	2017	10	7	0.613	0.045	18
annual	White-tailed Deer	adult	male	2017	10	8	0.613	0.046	22
annual	White-tailed Deer	adult	male	2017	10	9	0.639	0.040	157
annual	White-tailed Deer	adult	male	2018	11	1	0.753	0.031	29
annual	White-tailed Deer	adult	male	2018	11	10	0.730	0.034	63
annual	White-tailed Deer	adult	male	2018	11	11	0.717	0.043	133
annual	White-tailed Deer	adult	male	2018	11	3	0.817	0.024	130
annual	White-tailed Deer	adult	male	2018	11	7	0.777	0.028	18
annual	White-tailed Deer	adult	male	2018	11	8	0.769	0.029	49
annual	White-tailed Deer	adult	male	2018	11	9	0.744	0.033	185
annual	White-tailed Deer	adult	male	2019	12	1	0.743	0.039	29
annual	White-tailed Deer	adult	male	2019	12	10	0.717	0.042	82
annual	White-tailed Deer	adult	male	2019	12	11	0.710	0.046	125
annual	White-tailed Deer	adult	male	2019	12	3	0.826	0.029	127
annual	White-tailed Deer	adult	male	2019	12	7	0.747	0.038	18
annual	White-tailed Deer	adult	male	2019	12	8	0.737	0.040	81
annual	White-tailed Deer	adult	male	2019	12	9	0.721	0.042	157
annual	White-tailed Deer	adult	male	2020	13	1	0.753	0.059	60
annual	White-tailed Deer	adult	male	2020	13	10	0.755	0.058	77
annual	White-tailed Deer	adult	male	2020	13	11	0.765	0.057	123
annual	White-tailed Deer	adult	male	2020	13	3	0.843	0.042	113
annual	White-tailed Deer	adult	male	2020	13	7	0.768	0.055	18
annual	White-tailed Deer	adult	male	2020	13	8	0.755	0.058	69
annual	White-tailed Deer	adult	male	2020	13	9	0.767	0.055	149
annual	White-tailed Deer	adult	male	2021	14	1	0.680	0.058	90
annual	White-tailed Deer	adult	male	2021	14	10	0.583	0.091	75
annual	White-tailed Deer	adult	male	2021	14	11	0.733	0.051	123
annual	White-tailed Deer	adult	male	2021	14	3	0.795	0.043	113
annual	White-tailed Deer	adult	male	2021	14	7	0.745	0.049	18
annual	White-tailed Deer	adult	male	2021	14	8	0.749	0.049	66
annual	White-tailed Deer	adult	male	2021	14	9	0.666	0.068	149
annual	White-tailed Deer	juvenile	male	2013	6	10	0.389	0.082	41
annual	White-tailed Deer	juvenile	male	2013	6	11	0.341	0.081	33
annual	White-tailed Deer	juvenile	male	2014	7	1	0.405	0.064	25

annual	White-tailed Deer	juvenile	male	2014	7	10	0.292	0.049	32
annual	White-tailed Deer	juvenile	male	2014	7	11	0.236	0.048	49
annual	White-tailed Deer	juvenile	male	2014	7	7	0.330	0.058	28
annual	White-tailed Deer	juvenile	male	2015	8	1	0.658	0.041	21
annual	White-tailed Deer	juvenile	male	2015	8	11	0.494	0.050	63
annual	White-tailed Deer	juvenile	male	2015	8	3	0.505	0.057	38
annual	White-tailed Deer	juvenile	male	2015	8	7	0.555	0.047	23
annual	White-tailed Deer	juvenile	male	2015	8	9	0.559	0.047	53
annual	White-tailed Deer	juvenile	male	2016	9	11	0.470	0.054	88
annual	White-tailed Deer	juvenile	male	2016	9	3	0.425	0.058	47
partial year	White-tailed Deer	juvenile	male	2016	9	8	0.832	0.024	22
annual	White-tailed Deer	juvenile	male	2016	9	9	0.527	0.047	62
partial year	White-tailed Deer	juvenile	male	2017	10	10	0.884	0.017	35
annual	White-tailed Deer	juvenile	male	2017	10	11	0.446	0.046	74
annual	White-tailed Deer	juvenile	male	2017	10	3	0.418	0.045	60
partial year	White-tailed Deer	juvenile	male	2017	10	8	0.860	0.020	32
annual	White-tailed Deer	juvenile	male	2017	10	9	0.506	0.042	67
partial year	White-tailed Deer	juvenile	male	2018	11	10	0.878	0.022	35
annual	White-tailed Deer	juvenile	male	2018	11	3	0.382	0.062	45
partial year	White-tailed Deer	juvenile	male	2018	11	8	0.845	0.026	39
annual	White-tailed Deer	juvenile	male	2019	12	1	0.385	0.117	38
annual	White-tailed Deer	juvenile	male	2020	13	1	0.710	0.107	41

Chapter 3. A time-series survival model to measure habitat quality from demographic outcomes

Abstract

Habitat quality can be defined as the effect of habitat on demographic outcomes, and it is often argued that habitat quality should be measured in this way. However, making the connection between habitat use and demographic outcomes has been limited by both technology and a lack of analytical frameworks that allow this connection to be made explicitly. We present a novel modeling framework to measure habitat quality by its effect on demographic outcomes. We developed an autoregressive hierarchical model that uses observed GPS locations and survival state (alive/dead), to model the unobservable probability of survival as it changes with habitat use. Our Survival and Habitat Quality (SHQ) model quantifies the effects of varying quantity or quality of different resources on an individual's survival probability over time. This framework allows researchers to quantify the cumulative effects of factors such as nutrition and harsh weather on survival, while allowing for spontaneous factors such as predation or vehicle collisions.

Introduction

Habitat quality has long been noted as a driver of population dynamics, with different quality habitats conferring different levels of fitness on the individuals that use them (Fretwell and Lucas 1970). Building from this idea, Johnson (2007) defined habitat quality as an individual's "per capita contribution to population growth expected from a given habitat." By this definition, a habitat's quality should be measured by a change in population demographic rates, including survival and reproduction (Johnson 2007). However, habitat quality is rarely measured by demographic rates because of several limiting factors.

The first factor limiting the application of measuring habitat quality through demographic rates is sample size. Survival models (e.g., known fate, Cormack-Jolly-Seber, Cox proportional hazards, etc.) relate environmental variables to survival probability at discrete points in time, thereby establishing the link between habitat and population demographics. However, long-term datasets are necessary to capture temporal variation in habitat and survival rates, particularly for long-lived species (Johnson 2007). Additionally, long-lived species tend to have relatively little variation in adult survival (Gaillard et al. 1998), so large datasets with many individuals must be collected to estimate the survival rate precisely. However, with the advent of global positioning system (GPS) collars, collecting survival information and animal locations on a large scale is much more feasible than ever before and appropriately large datasets are more common.

When sufficiently large datasets can be collected, analytical limitations are a second obstacle in connecting habitat quality to population demographics. When survival models connect animal mortality to environmental conditions at the time of death, inference is limited to the proximal cause of death, which may not reflect the ultimate cause if it occurs on a longer timeframe. For example, poor quality habitat can lead to malnourishment and then to death, but the environmental conditions in the death site may or may not reflect the conditions that led the animal to its malnourished state. Because we can observe only the outcome of survival (alive or dead) rather than survival probability itself, it is challenging to account for cumulative processes that lead to an animal’s death. Existing survival models require lag effects to account for these mismatched time scales, but the time frame of a lag effect is difficult to define and can be arbitrary.

Here we present a model that relates survival to more environmental conditions than only those experienced at a single moment specified in time. Instead, it relates survival to the accumulation of resources over an individual's lifetime. Building from existing survival models, the Survival and Habitat Quality (SHQ) model introduces an autoregressive process model that is a more realistic representation of how resources contribute to long-term survival. By removing the assumption of independence over time from existing survival models, it models the survival *process* rather than simply trying to measure or predict the *outcome* of survival. Using observed GPS locations and survival states (alive or dead) to model an individual’s unobservable, time-varying survival probability, the SHQ model measures the quality of a given habitat patch by the amount its resources increase or decrease an individual’s probability of survival over time. The SHQ model therefore allows inference to the ultimate causes of mortality from long-term processes like nutrition and disease exposure.

In this chapter, we develop the SHQ model conceptually and validate it using simulated data where habitat quality is known. In natural environments, many factors affect survival to varying degrees; some have strong effects, and some have weak effects. Traditional survival models may detect strong effects on a short time scale but are unlikely to detect weak effects. We demonstrate the model’s ability to detect small and large effects of resources on survival under perfect detection and with missing data.

Methods

Model development

The Survival and Habitat Quality (SHQ) model defines the quality of a habitat patch by its cumulative effect on an individual's probability of survival. It is an autoregressive, discrete time survival model that uses observations of y_{it}, the state (alive or dead) of individual i at time t. For each individual, the model is defined for every occasion the individual is alive from capture (C_i) until death or censoring (D_i). Censoring occurs when an individual's collar fails or the study ends. L_i, an individual's lifespan over the study (i.e., the number of discrete occasions alive) is therefore calculated as

$$L_i = D_i - C_i + 1 \tag{Eq. 1}$$

The model is conditional on capture, so when the model is defined from $t = 1, \ldots, L_i$ for each individual, individuals are known to be alive ($y_i = 1$) at $t = 1$, and therefore the probability of survival on the first occasion, $S_{i1} = 1$. For every occasion from $t = 2, \ldots, L_i$, the alive/dead state y_{it} is drawn from a Bernoulli distribution, which is defined by survival probability, S_{it}, and the individual's previous state (alive = 1 or dead = 0)

$$y_{it} \sim Bern(S_{it} \cdot y_{i(t-1)}). \tag{Eq. 2}$$

The Markovian dependence on the individual's previous alive/dead state allows for imputation on occasions in which the alive/dead state is unobservable; it maintains dead animals in the dead state (survival probability on all future occasions is 0) and live animals in the live state with probability S_{it}. The probability of survival, S_{it}, is then defined by the habitat quality experienced by the individual on that and all previous occasions. We represent habitat quality of a patch experienced by individual i at time t using the linear model $X_{it}\beta$, where X_{it} is a vector of covariates representing resource quality or quantity at the individual's location at time t and β is the vector of coefficients defining the effect size of each covariate

$$logit(S_{it}) = \alpha_{i0} + \sum_{k=2}^{t} X_{ik}\beta\,,\ t = 2, \dots, L_i \qquad \text{(Eq. 3)}$$

Because habitat use prior to capture is not known, we model an individual's initial survival probability using a random effect (α_{i0}) with mean μ_0 and standard deviation σ_0

$$\alpha_{i0} \sim N(\mu_0, \sigma_0). \qquad \text{(Eq. 4)}$$

The autoregressive component allows survival probability to continually decrease with time spent in low-quality habitat and to increase with time spent in high-quality habitat. The logit transformation asymptotes near 0 and 1, meaning that an individual in very good condition with a high survival probability near 1 will only benefit marginally from continued use of high-quality habitat, but an individual with a survival probability nearer to 0.5 will benefit to a much greater degree. In this way, we model the unobservable process of survival (or ultimate, rather than proximal, cause of death) mechanistically as a function of habitat use.

Although survival probability is defined by habitat use, there is always some probability that an individual will die ($S_{it} < 1$), regardless of the quality of its current habitat or its history, so randomness can dictate the proximal cause of death. Alternatively, the model in Eq. 3 can be modified to accommodate environmental variables that represent acute risk but do not affect probability of survival long-term. For example, crossing a road may only present a short-term risk to an individual without causing chronic stress. Acute effects are added in a linear model to Eq. 3

$$logit(S_{it}) = \alpha_{i0} + \sum_{k=2}^{t} X_{ik}\beta + W_{it}\theta \qquad \text{(Eq. 5)}$$

where W_{it} is a vector of acute covariates and θ is the vector of effects parameters.

Simulation

We tested the SHQ model with simulated data using R version 4.1.3 (R Core Team 2022). We first simulated a landscape of distinct habitat patches, where habitat quality was known for each patch. We defined habitat quality in each patch (Q_c) via a linear model on five simulated covariates plus some additional unobserved error (Eqs. 6 – 7).

$$Q_c = -0.6X_{1c} - 0.08X_{2c} + 0X_{3c} + 0.08X_{4c} + 0.6X_{5c} + \varepsilon_c \qquad \text{(Eq. 6)}$$

$$\varepsilon_c \sim N(0, 0.1) \qquad \text{(Eq. 7)}$$

We chose effect sizes of -0.6, -0.08, 0, 0.08, and 0.6 to test the model's ability to detect small and large effects – in both negative and positive directions – as well as no effect. We simulated covariates that were centered and scaled, so larger effect sizes represented resources with higher relative importance. The value of 0.6 reflected a large possible change in daily survival rate for a long-lived species and 0.08 reflected a small but meaningful possible change in daily survival rate on the logit scale. For example, given a baseline daily survival rate of 0.9994 (annual survival 0.803), an increase of 0.6 on the logit scale increases daily survival rate to 0.9997 (annual survival 0.887), and an increase of 0.08 increases daily survival rate to 0.99945 (annual survival 0.817).

We then simulated 300 animals that randomly selected one of 1000 habitat patches at each of 300 discrete temporal occasions. Each individual's initial survival probability was drawn from a normal distribution centered on 0.9994 with a standard deviation of 0.2. These values were chosen to represent individual heterogeneity in daily survival probability of a long-lived species. At the following time step, $t = 2$, survival probability increased or decreased from its initial survival probability, depending on the quality of the patch experienced at $t = 2$. At all subsequent time steps, the individual's survival probability increased or decreased from the previous occasion depending on habitat quality of the patch the individual occupied at time t. After simulating each individual's time-varying survival probability, we simulated the individual's state (alive or dead) from the Bernoulli distribution defined by the individual's survival probability at time t and whether the individual was alive ($y = 1$) or dead ($y = 0$) at the previous time step (Eq. 2).

To validate the model, we first simulated 10 data sets with no missing observations, and we estimated the β parameters for each replicate data set using NIMBLE version 0.12.2 (de Valpine et al. 2022). We used uninformative priors on the mean and standard deviation of α_{i0}, as well as on the β parameters (see Appendix 3.1). For each model run, we ran three chains for 50,000 iterations, with the first 10,000 discarded as burn-in. We assessed convergence visually by inspecting the MCMC plots for chain mixing and analytically through R-hat values of <1.1.

To validate the model when an individual's location and alive/dead state could not always be observed, we incorporated missing observations into 10 additional simulated data sets. We randomly assigned approximately 10% of all individuals' locations to be missing, and we replaced X_{it} and y_{it} with NA values on those occasions. To allow the model to integrate over all possible values of the environmental covariates, we defined prior distributions for our missing values of X_{it} (Appendix 3.1). Estimating parameters when some observations were missing took much longer computationally, so we reduced our simulated data for this analysis to 150 occasions in each data set. We also used a slightly informative prior on μ_0 (Appendix 3.1). For each of the 10 simulated data sets, we ran the model for 30,000 iterations, and discarded the first 10,000 as burn-in.

Results

For our simulation without missing observations, the model-estimated 95% Bayesian Credible Interval (BCI) captured the true value of the habitat quality parameters for 98% of the parameters across the 10 replicates (Figure 3.1). Between the large and small parameters (excluding the 0 effect parameter), the BCI did not overlap 0 for 97.5% of estimates, indicating precision in estimation. We recorded a slight negative bias in estimates of negative parameters but a slight positive bias in estimates of positive parameters (Table 3.1).

When we ran the model on datasets with 10% of observations missing, the model performed similarly in terms of coverage; the true value was captured within the BCI for 92% of the parameter values across the 10 replicates (Figure 3.2). Estimates were somewhat less precise, with 88% of BCIs for non-0 effect sizes not overlapping 0. Recorded bias in parameter estimates was in the opposite direction from the model with no missing observations; there was a slight positive bias for negative parameters and a slight negative bias for positive parameters (Table 3.1).

Chain convergence of all parameters was achieved for all 10 of the model runs for datasets without missing observations, but only 6 of the 10 replicates for datasets with missing observations. For those replicates that did not converge, R-hat values near 1.1 indicated that the models were close to convergence, but small values of effective sample size indicated models needed to be run for more iterations to achieve more consistent convergence.

Discussion

The SHQ model provides a new framework for defining habitat quality from processes that accumulate over an individual's life. By defining survival through the combination of past experiences, current conditions, and luck, it establishes a more biologically realistic model of processes that occur on long time scales, such as malnutrition, chronic stress in a landscape of fear, and exposure to disease risk. By viewing survival probability as a cumulative process rather than a quantity to be estimated at discrete time points, it removes the necessity of defining lag effects for processes that occur at long time scales. Additionally, the cumulative nature of the model allows for individual differences in responses to habitat quality, as individuals in worse condition have more to gain from high quality resources than individuals with an already-high survival probability do. Rather than complicating the model, variation in conditions experienced between individuals and over time increases the observed variability in covariate values and therefore improves parameter estimation.

The SHQ framework is flexible enough to apply to a wide variety of species and ecosystems. Habitat quality, as defined in Eq. 3, is made up of a combination of resources defining a habitat patch at a given point in time, and these resources can be measured by their quality or quantity. Some examples of resources include nutritional quality (perhaps represented by forage greenness for herbivore species), food quantity (e.g., biomass), exposure to disease (e.g., relative abundance of disease vectors), and predation risk (e.g., number of predators present). Quadratic effects could be added for resources that are hypothesized to have highest quality in mid-range values. Additionally, interaction effects could be included to account for resources whose quality changes due to other variables. For example, in an arid environment, water sources can be highly important to survival, but in disease outbreak years, water sources may congregate individuals and increase transmission, thereby making water sources a lower quality habitat in these years (Berry et al. 2013). An interaction effect of water availability and disease outbreak could capture this complexity. Finally, the short-term and long-term combination model specified in Eq. 5, may allow researchers to tease apart ultimate versus proximate causes of mortality (e.g., comparing long-term effects of nutrition or chronic stress to short-term risks like predation or vehicle collision).

Because the SHQ model defines habitat quality through its impact on a demographic outcome, it explicitly measures the effect of habitat on population dynamics, rather than assuming a demographic outcome from behavior. In contrast to resource selection functions (RSFs), the SHQ model measures the habitat quality of locations used by animals without making any assumptions about the motivations behind the choice to use that location (Buskirk and Millspaugh 2006). The SHQ model does not assume that animals make every movement purposefully, nor does it assume that animals make rational decisions with perfect knowledge of the landscape, such as assessing tradeoffs between nutrition and predation risk. The same model applies equally well to "lucky" individuals that happen to live in ideal conditions for its species, "smart" individuals that make the best choices given their surroundings, "unlucky" individuals that experience stochastic events (such as major storms, vehicle collisions, or hunter harvest), and "dumb" individuals that make imperfect decisions. The SHQ model allows researchers to differentiate between these different categories of experiences, rather than making assumptions of habitat quality based on behavior.

Habitat quality estimators that use GPS locations assume that GPS fixes represent used resources, which may not always be true. For example, for an individual fleeing a predator, available food resources are irrelevant and remain unused. GPS fixes do not differentiate between an individual using a habitat patch to flee and an individual using the habitat patch for nutritional benefit. To help differentiate between behaviors, it may be possible to incorporate staying time into the SHQ model to help provide context for animal behavior and level of use. Additionally, it could be useful to model animals' movement to better inform habitat use between GPS fixes. Using a movement model may improve the precision of parameter estimation when some locations are missing; instead of integrating over all possible resource values that could have been experienced qualities, the model could be limited to exploring the values from areas available to the individual.

The SHQ model provides an estimate of habitat quality based on survival and allows inference to the habitats that support the healthiest animals by this metric. Individuals with access to a high quality or quantity of nutrition tend to have better body condition, which affords them a higher survival probability. Meanwhile, individuals without proper nutrition can get weaker over time and become more susceptible to disease, predation, and the effects of malnutrition, so their survival probability decreases. However, survival alone does not paint the entire picture of habitat quality without knowledge of reproduction and abundance (van Horne 1983). Areas with high survival and high abundance may have low reproduction rates as a result of density dependence (Hobbs and Hanley 1990). Alternatively, two habitats with equal survival rates may support different animal densities, with the higher quality habitat supporting higher density. A more holistic and accurate estimate of habitat quality could be attained if reproduction and abundance were also included as response variables in an integrated model (van Horne 1983, Johnson 2007).

When used in conjunction with other analytical techniques such as RSFs or home range analyses, the SHQ results could yield critical insight for habitat management and conservation. For example, the results of the SHQ model allow the creation of predictive maps of high- and low-quality habitats for the species of interest. When overlaid on a map predicting animal distribution or resource selection, areas with high animal selection but low survival could indicate habitat “sinks” or ecological traps and therefore priority zones for habitat management interventions (Kristan 2003). Such maps would also provide insight into the spatial arrangement of habitat quality and selection, which could be useful for managers tasked with redistributing wildlife to match human tolerances. Areas with differing levels of human conflict, animal survival, and selection may require different management approaches.

The SHQ model is general enough to be applied to any species with fine-scale location data. GPS collars and remote sensing data make application of the model feasible over large areas and long timeframes. Several distinctions between simulated data and real data may affect inference, so some practices should be kept in mind. First, our simulation allowed animals to randomly use habitat patches, regardless of spatial arrangement or quality. Real animals with movement constraints and decision-making abilities may experience less variation in habitat quality, which would reduce the model’s power to estimate effects. Temporal variation (e.g., due to seasons, storms, disease outbreaks, etc.) may be sufficient to overcome the decreased variation, particularly if collars are monitored over long time periods. Second, because habitat quality in the SHQ model is derived from the experiences of individuals, it is important that collared individuals represent the population as a whole. Habitat quality effects should be easier to detect with lower numbers of collared individuals if the study species is a specialist with low inter-individual variation than if the species is a habitat generalist (Boyce et al. 2002). Because the SHQ model was able to estimate habitat quality for simulated data, we proceed to Chapter 4 to test it on data collected from real animals.

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Tables

Table 3.1. Mean bias in estimates for 5 parameters across 10 replicated datasets, using no missing observations or with 10% of observations missing.

Parameter	Truth	Bias, no missing observations	Bias, 10% observations missing
B[1]	-0.6	-0.059	0.030
B[2]	-0.08	-0.007	0.005
B[3]	0	0.006	0.017
B[4]	0.08	0.008	-0.015
B[5]	0.6	0.055	-0.026

Figures

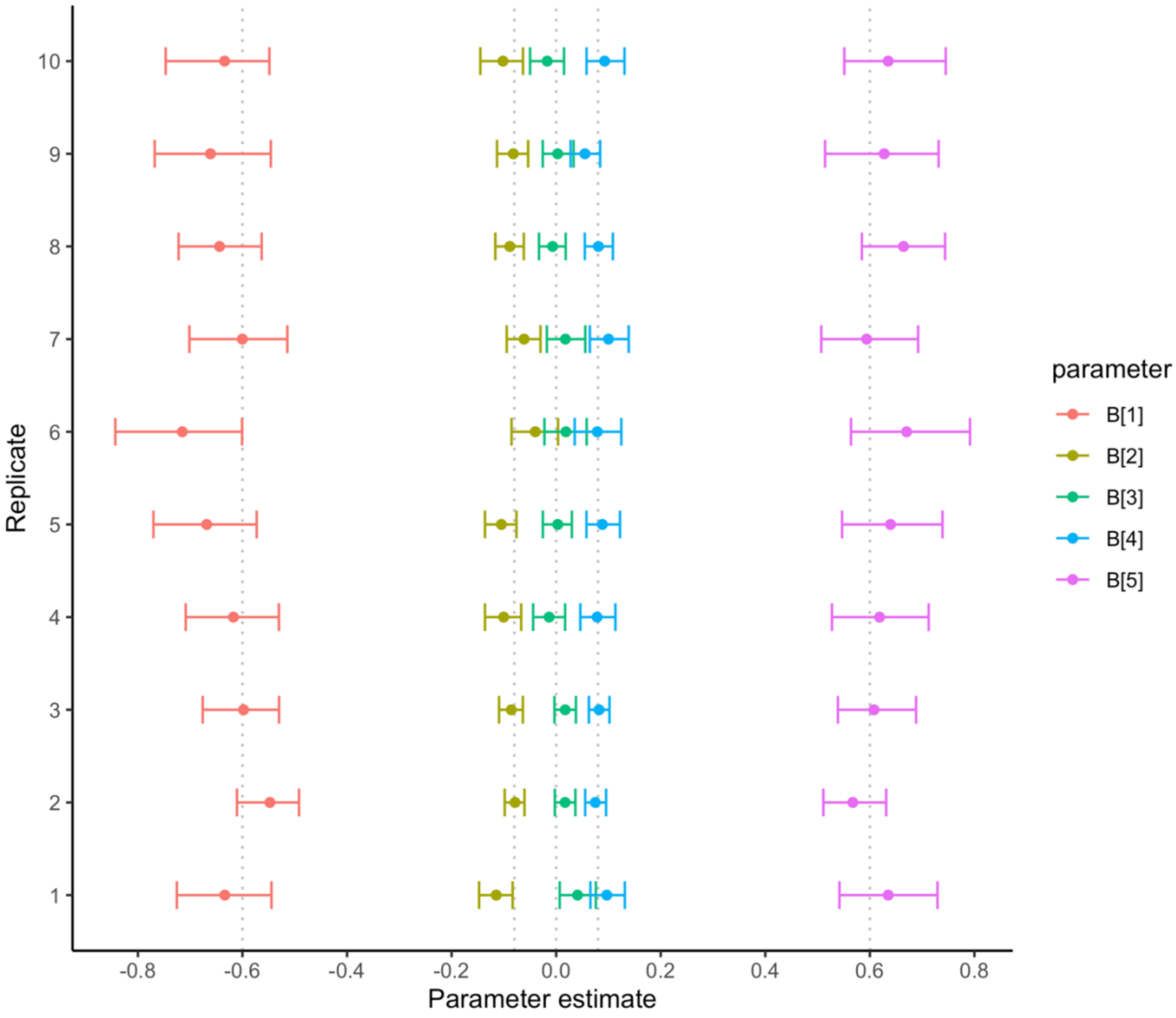

Figure 3.1 Mean parameter estimates and 95% Bayesian Credible Intervals from 10 simulated datasets without any missing data. Simulated ("true") values of parameters represented by dotted gray lines.

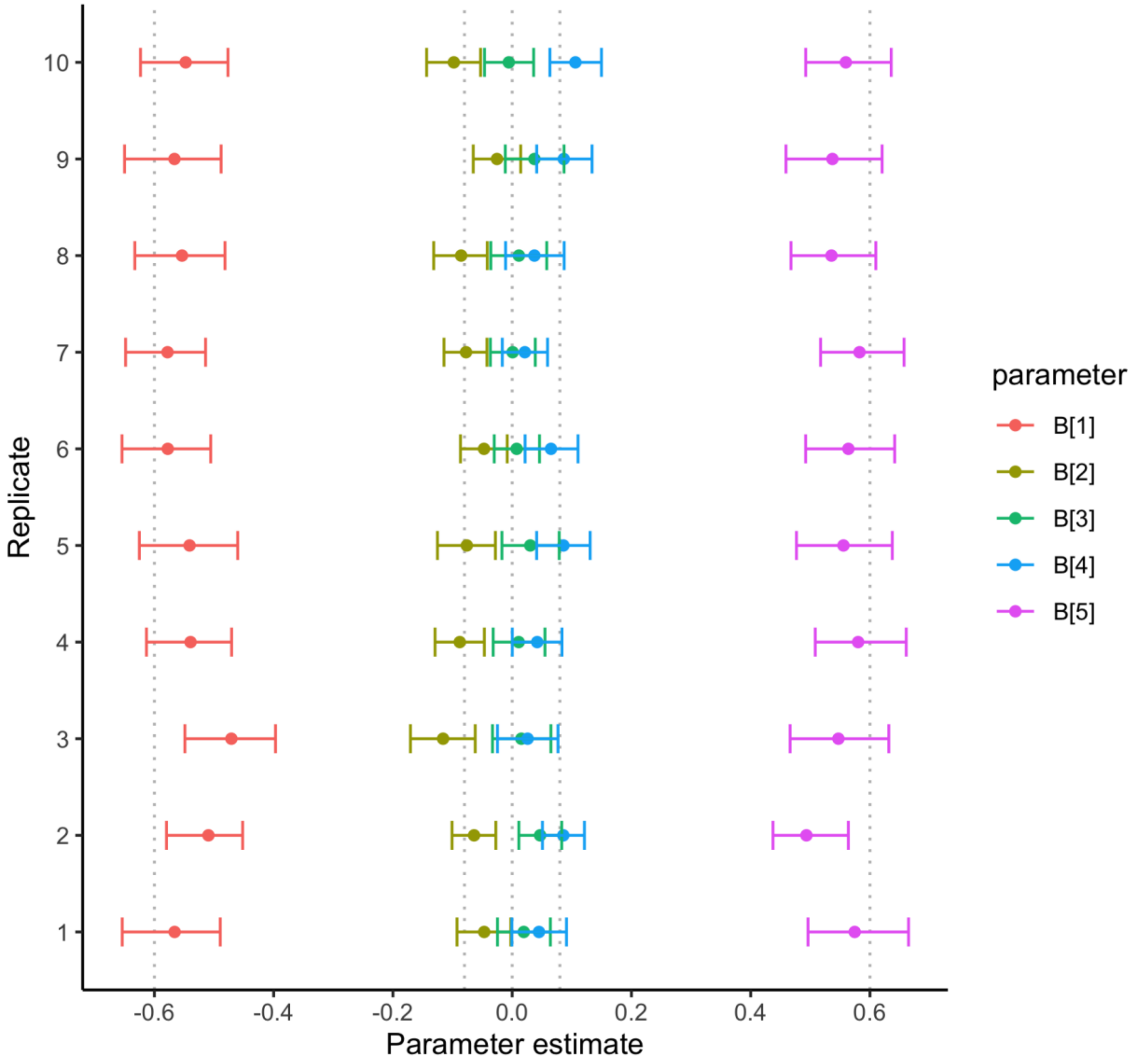

Figure 3.2. Mean parameter estimates and 95% Bayesian Credible Intervals from 10 simulated datasets, with approximately 10% of observations missing. True values represented by dotted gray lines.

Appendix 3.1. Survival and Habitat Quality model BUGS code

```
model{
 # Priors
 # Centered on 0.99
 beta0.mu ~ dnorm(log(0.99/(1 - 0.99)), 0.05)T(-10, 10) # Uninformative prior no
missing data
#  beta0.mu ~ dnorm(log(0.99/(1 - 0.99)), 2)T(-10, 10) # More informative prior -
missing data
 beta0.tau <- 1/(beta0.sd * beta0.sd)
 beta0.sd ~ dunif(  0, 2 )
 for(i in 1:nind){
   b0[i] ~ dnorm( beta0.mu, beta0.tau )
 }
 for(c in 1:ncov){
   B[c] ~ dnorm(0, 0.001)T(-10, 10)
 }

 # Likelihood
 for(i in 1:nind){
   # First time step
   Smu[i, f[i]] <- b0[i] # individual intercept
   # Future time steps
   for(t in ((f[i])+1):(d[i])){
     Smu[i, t] <- Smu[i, t-1] + (X[i,t,] %*% B[])[1,1]
   }
   for(t in (f[i]):(d[i])){
     # Transform to 0-1 scale
     logit(S[i, t]) <- Smu[i, t]
   }
 }

 # Survival
 for(i in 1:nind){
   y[i, f[i]] <- 1
   for(t in (f[i]+1):d[i]){
     muS[i, t] <- S[i, t] * y[i, t-1]
     y[i, t] ~ dbern(muS[i, t])
   }
 }

 # Data likelihood for any missing observations

 for(i in 1:nind){
   for(j in f[i]:d[i]){
     for(c in 1:ncov){
```

```
        X[i,j,c] ~ dnorm(0, 1)T(-5, 5) # centered and scaled covariates
      }
    }
  }
}
```

Chapter 4. Novel method quantifies habitat quality and survival of mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*)

Abstract

Changes in habitat quality and quantity may be a consistent underlying factor driving or exacerbating mule deer population declines and concurrent white-tailed deer population increases. However, understanding what constitutes high quality habitat for mule deer and white-tailed deer is challenging, due to limitations of technology, sample size, and analytical frameworks. Leveraging one of the largest existing long-term datasets of GPS collared mule deer and white-tailed deer, we applied the newly developed Survival and Habitat Quality (SHQ) model to measure habitat quality through different resources' effects on survival. Over three years, we estimated survival and habitat quality for adult females and juveniles of both species. Juvenile deer had more variation than adults in their responses to elevation, slope, drought, perennial forbs and grasses, annual forbs and grasses, and shrubs. Juvenile mule deer had the strongest responses to habitat variables of any group, showing increased survival in areas of higher elevation, lower slope, more shrubs, and less production of annual forbs and grasses. The SHQ model gave inference into long-term effects of habitat on individual survival, thereby connecting habitat quality to an important metric of population performance. Predictive maps of habitat quality will help managers highlight areas of conservation priority for mule deer.

Introduction

Across their range, mule deer (*Odocoileus hemionus*) populations appear to have been declining for decades (Wallmo 1981). Concurrently, white-tailed deer (*O. virginianus*) populations are expanding into new areas not previously part of their range and are highly abundant in many areas (VerCauteren 2003). In the two species' sympatric range, many wildlife managers are concerned about these long-term patterns and are interested in increasing mule deer populations and decreasing white-tailed deer populations (Carpenter 1997). However, despite decades of research, the underlying driver of these patterns is still not clear, making management difficult. Numerous hypotheses have been proposed for the patterns, including differing effects on the two species of predators, weather, hunting, livestock, competition, disease, and habitat changes, but no single hypothesis has emerged with strong support across time and space (Anderson et al. 2012, DeVivo et al. 2017). Indeed, multiple factors may be occurring at once, making it hard to separate out a single driver. However, rapid changes in habitat quality and quantity may be a consistent underlying factor driving or exacerbating changes in population trajectory (Carpenter 1997).

A clear understanding of habitat quality is critical for disentangling drivers of population change. However, understanding what constitutes high quality habitat for mule deer and white-tailed deer is challenging. Mule deer and white-tailed deer habitats are typically differentiated, with white-tailed deer described as using more tree cover and agriculture and mule deer using higher elevations and rangeland (Wood et al. 1989, Whittaker and Lindzey 2004). However, the two species have a high degree of overlap in habitat selection and diet (Martinka 1968, Anthony and Smith 1977, Smith 1987, Lingle

2002, Whittaker and Lindzey 2004). Additionally, both species can be described as habitat generalists because their ranges encompass dramatically variable climatic, physiographic, and biological features. Together, these factors make it difficult to define high- and low-quality habitat for each species.

Limitations of technology, sample size, and analytical tools also make it difficult to define and measure habitat quality of any species. Habitat quality should be measured by population-level changes in demographic rates including survival, reproduction, and abundance (Johnson 2007). However, long-term datasets with sufficient data to estimate these demographic rates are hard to come by. Estimating survival of a long-lived ungulate species requires huge monitoring datasets of many individuals across many years. However, the relatively recent expansion in use of global positioning system (GPS) collars now allows biologists to collect large, fine-resolution datasets of individuals' locations and to monitor survival of many individuals without extensive field time. Yet, the price tag of capturing and collaring many individuals is prohibitive in many cases.

Even when sufficient sample sizes for estimating survival can be obtained, available analytical tools limit the conclusions that can be made about habitat quality. Traditional survival models (e.g., known fate, Cormack-Jolly-Seber, Cox proportional hazards) relate environmental conditions experienced by animals to their survival state (alive or dead). In doing so, they are designed to make inference only to a resource's effect on survival at a single point in time. Long-term effects are captured with lag effects, although the appropriate time scale of lag effects can be very hard to define. Even with large datasets consisting of many individuals monitored for multiple years, these models cannot differentiate between an individual in good condition that dies in a low-quality or risky habitat from an individual in poor condition that dies from nutritional stress but is located in high-quality habitat at the time of death. The mortality locations of both individuals will be observed as poor habitat. This is a fundamental deficiency with the current state of survival and habitat modeling.

The newly developed Survival Habitat Quality (SHQ) model from Chapter 3 addresses the analytical issues inherent to other survival models by incorporating an animal's entire history of resource use and the cumulative effects of those experiences. The SHQ model is a Bayesian hierarchical model that uses observed GPS locations and survival state (alive/dead), to model the unobservable probability of survival as it changes with resource use. It is a time-series survival model that quantifies the cumulative effect of resource quantity or quality on an individual's survival probability over time. This approach contrasts with traditional survival models in that it models the survival *process* rather than measuring or predicting the survival outcome. By defining habitat quality via a change in survival probability, this framework allows researchers to quantify the cumulative effects of factors such as nutrition and harsh weather on survival, while also allowing for spontaneous factors such as predation or vehicle collisions. The results allow biologists to directly compare the quality of different resources on the landscape and to build predictive maps of habitat quality for a given species, which then enables managers and conservationists to identify target areas for habitat manipulation.

Our aim in this study was to quantify the habitat quality available to sympatric populations of mule deer and white-tailed deer. We capitalized on one of the largest long-term datasets of GPS collared deer in their sympatric range and used the newly developed SHQ model to measure habitat quality through different resources' effects on survival.

We tested six factors that we hypothesized may differentiate habitat quality of mule deer and white-tailed deer: elevation, slope, drought, and net primary productivity of three different plant functional groups (annual forbs and grasses, perennial forbs and grasses, and shrubs). We compared the effects of each resource on the survival probability of juveniles and adult females of both mule deer and white-tailed deer. Our results shed new light on habitat quality for North American deer and provide managers with a new way to prioritize habitat management interventions.

Methods

Study area

We conducted the study in northwestern South Dakota, USA (Figure 4.1; 44°57'8" – 45°56'43" N, 100°18'31" – 104°2'44" W). Our study area was one of 11 data analysis units (DAU) which designate deer populations based on climate, geographic factors, and management (South Dakota Department of Game Fish and Parks 2017). Our study area, DAU 1 (~21,160 km^2), was dominated by mixed-grass prairie and agricultural crops, and the land was a mixture of private and public ownership. The 15-year mean temperatures in this area ranged from -7°C in February to 23°C in August and mean precipitation ranged from 0.5 cm in January to 8.9 cm in May (National Climatic Data Center 2022). Elevation ranged from 490 m to 1173 m. In addition to mule deer and white-tailed deer, pronghorn (*Antilocapra americana*) were common and elk (*Cervus canadensis*) were present but rare. The most common predators of deer in the study area were coyotes (*Canis latrans*) and bobcats (*Lynx rufus*).

Capture, collaring, and monitoring

Over the winters of 2019, 2020, and 2021, we captured and collared 345 mule deer and 345 white-tailed deer using helicopter net-gunning (Table 4.1). We captured juvenile males and females (<1 year-old) and adult females (>1 year-old) of both species, following the American Society of Mammalogists' guidelines for animal capture and handling (Sikes et al. 2016). Protocols were approved by University of Montana Institutional Animal Care and Use Committee (064-18PLWB-121418). We aimed for even spatial representation of collars on both species across the study area and tried to collar individuals from different groups. Collars functioned for multiple years, and if recovered from mortalities they were redeployed on new individuals. We outfitted 135 of the 690 deer with GPS collars manufactured by Vectronic Aerospace GmbH (Berlin, Germany), which used the Iridium satellite system and took positions every 5 hr. The other 555 deer received GPS collars from Telonics, Inc. (Mesa, Arizona, USA) that used the GlobalStar satellite system and took positions every 5 hr (n = 81), 11 hr (n = 279), or 13 hr (n = 195). Female deer received non-expandable collars (495 – 560 g), and male deer received expandable collars (270 – 365 g) to allow for neck expansion during the rut. For juveniles of both sexes, we padded the collars with temporary foam to allow for growth during aging.

When our GPS collars sent mortality messages via satellite, an observer located the collar within several days and investigated the site for signs of mortality (evidence included blood, bones, and hair) or for a broken or slipped collar. Once we retrieved a collar, we backdated mortality or collar failure to the date the mortality signal was first transmitted.

Habitat quality survival model

We assessed survival probability and habitat quality using the Survival and Habitat Quality (SHQ) model developed in Chapter 3. In the model, daily survival probability for each individual is dependent on survival probability from the previous day and the habitat quality experienced on the current day. The model assumes that each resource has a linear relationship with its effect on survival. Habitat quality (Q) of any location c at time t is defined by the linear model

$$Q_{ct} = \boldsymbol{X}_{ct}\beta + \varepsilon_c \qquad \text{(Eq. 1)}$$

where $\boldsymbol{X}$ is a vector of values of environmental covariates at location c, β is the effect of each environmental covariate on the logit-transformed daily survival probability, and ε is normally distributed error. Habitat quality is defined as the amount that a location increases or decreases an individual's daily survival probability. This effect is cumulative; an individual that stays in a low-quality location will have its survival probability reduce every day. Because survival probability is logit-transformed, the same habitat cell will decrease or increase survival probability most if the individual has a daily survival probability around 0.5; as daily survival probability gets closer to 1 or 0, the habitat will have a smaller effect on survival probability (Figure 4.2).

Preparing encounter histories

We used GPS data from January 2019 – December 2021 for our analysis. We made daily survival encounter histories for each collared deer during this study period. We designated mortalities that occurred within 14 days of capture as being capture-related, and we excluded these individuals from analyses (Chalmers and Barrett 1982). We started each individual's encounter history two days after its capture date to allow deer adequate time to return to normal habitat use and movement behavior. We right-censored individuals that died by hunter harvest or whose collars stopped functioning, so survival rates were interpreted as the probability of survival in the absence of hunting. To standardize across our different collar fix rates, we subset our data to one GPS fix per individual per day, which we selected randomly from the fixes taken each day.

We defined juvenile survival from January 1 to May 30, and we interpret juvenile survival results as overwinter survival probability. Juveniles that were still alive on June 1 were assigned to the adult age class from then on and were used to fit adult models. We defined adult survival from January 1 to December 31 each year. Because the SHQ model is a time-series model, long encounter histories increase the complexity and total computational load. To increase our adult sample size and decrease computational load, we made encounter histories for each individual in each year it was alive. Thus, an individual that was alive and on-air during our entire 3-year study appeared in the encounter history three times.

We determined whether individual was alive on a daily basis (recording 1 if alive and 0 if dead). If no GPS fixes were taken on a given day, we recorded the day as missing data (NA). Our model accounted for missing data by integrating over all possible encounter histories. We assumed that survival states, when observed, were assigned without error, so we assigned any missing data between "alive" observations as "alive". We did not change any missing observations that preceded a "death" observation or the end of the encounter history. We removed 23 of the total 1,239 encounter histories (1.8%) that consisted of more than 20% missing data.

Measuring habitat variables

To measure the habitat experienced by each individual on each day, we extracted the values of remote sensing layers to each individual's one daily GPS location. Because we measured survival on a daily basis, we imposed a grid on the study area with a grid cell size defined by the average distance moved per day. To estimate average daily distance, we first calculated movement speed for each individual between subsequent GPS locations (using all locations, not just one per day) by dividing the distance between points by the time elapsed. We then obtained an estimate of daily movement by multiplying each individual's hourly movement speed by 24 hours. Across all our individuals, we calculated the median daily distance traveled as 1,569 m. Using this value as the hypotenuse of a square, we determined that the appropriate grid cell was approximately 1,110 x 1,110 m.

We accessed remote sensing data for elevation, slope, drought, net primary production (NPP) of perennial forbs and grasses (PFG), NPP of annual forbs and grasses (AFG), and NPP of shrubs using Google Earth Engine (Gorelick et al. 2017). For elevation and slope, we used the 10m resolution 3D Elevation Program Digital Elevation Model (U.S. Geological Survey 2019). To represent drought, we used the Palmer Drought Severity Index (PDSI) from the daily, 4-km resolution Gridded Surface Meteorological (GRIDMET) dataset (Palmer 1965, Abatzoglou 2013). We obtained our three NPP variables (PFG, AFG, and shrubs) from the annual, 30m resolution Rangeland

Analysis Platform (USDA Natural Resources Conservation Service et al. 2019, Robinson et al. 2019).

Because our habitat variables had different resolutions than our target grid cell size, we aggregated each remote sensing dataset to the designated cell size. For each environmental variable, we calculated new cell values from the mean of the original cells within each new 1,110 x 1,110 m grid cell. For each daily location for each individual, we extracted the value of the corresponding environmental variables for use in our analysis. To aid in interpretation of our results, we centered and scaled all variable values we experienced by deer during our study. The six variables we tested were not strongly collinear ($R^2 < 0.5$ for all pairs).

Analysis

To compare and contrast habitat needs across species and age classes, we ran the SHQ on four separate groups: mule deer juveniles (males and females combined), mule deer adult females, white-tailed deer juveniles (males and females), and white-tailed deer adult females. We ran the SHQ model on each species-age group using NIMBLE (de Valpine et al. 2017, 2022) in R version 4.1.3 (R Core Team 2022). For juvenile models, we ran three chains of 30,000 iterations each, with the first 10,000 discarded as burn-in. Adult models were much more computationally complex due to the longer encounter histories and had a correspondingly long run time, so we ran three chains of 10,000 iterations each, with the first 2,000 discarded as burn-in. For all models, we checked for convergence visually using trace plots and numerically by Rhat values < 1.1 (Gelman and Rubin 1992).

Using the SHQ model, we estimated each individual's survival probability on each day based on current and previous environmental conditions as well as the individual's unknown initial survival probability. We formulated initial survival probability as an individual-varying random effect. We used informative priors for the random effect because deer are long-lived species and daily survival probability is generally high, with juvenile survival lower and more variable than adult survival (Gaillard et al. 1998). We modeled the mean of the random effect as a normal distribution centered on 0.99, with a standard deviation of 0.7 (for adults) or 1.4 (for juveniles). We fixed the standard deviation of the random effect at 1 for all groups except white-tailed deer juveniles, which we set at 2; all were based on estimates of standard deviation obtained from initial model runs.

We used uninformative priors for the effects of the environmental variables. We expected the effect sizes to be small, given we were monitoring effects on daily survival. To allow the MCMC to explore a wide range of values, we used normal priors centered on 0 with a standard deviation of 1.7, but we defined our parameters in the model as 1/100 of that value. Because the environmental variables were centered and scaled, we used standard normal distributions as priors for any missing data points.

Results

Mortalities

We recorded 275 natural (non-hunting) mortalities from the 630 deer used in our analysis. Of these, 69 mortalities were of mule deer juveniles, 63 were of mule deer adult females, 16 were white-tailed deer juveniles, and 127 were white-tailed deer adult females.

Site characteristics

We quantified the available values of each of our habitat variables in our study area and compared the use recorded by our collared individuals (Table 4.2). Both species of deer and both age classes used the full range of elevation and slope available. Both species and both ages used comparable values of PDSI, using all but the most extreme dry and wet values. PDSI values in our study area ranged from -5 to 14, with negative values representing drier conditions than normal and positive values representing wetter conditions than normal. PDSI values below -5 indicate extreme drought and values above 5 are extremely wet conditions.

For two of our three NPP variables (AFG NPP and PFG NPP), we found that some recorded values were much higher than was realistic (see Discussion). Although the maximum AFG NPP value was 2955, the distribution was highly skewed and the value of the 99th percentile was only 486. Compared to the 99th percentile, mule deer juveniles and white-tailed deer juveniles used slightly smaller values of AFG NPP, and adults of both species used the full range of available values. The PFG NPP values were also higher than was realistic, but deer were recorded across all values. Finally, all species and ages used the smaller values of shrub NPP, with mule deer juveniles using the smallest range of values and white-tailed deer adult females using the largest range of values.

Mule deer juveniles

Mean daily survival probability for mule deer juveniles was 0.9950 (95% BCI 0.9936 – 0.9962). Mean 6-month overwinter survival probability was 0.404 (95% BCI 0.311 – 0.500).

Four of our six environmental variables had a measurable effect on mule deer juvenile survival (Figure 4.3a). The strongest effect on mule deer juvenile survival was NPP of annual forbs and grasses, with larger values of AFG NPP decreasing daily survival probability (mean -0.0303, 95% BCI -0.0464 – -0.0152). Holding all other habitat variables at their mean, an individual mule deer with the mean daily survival rate of 0.9950 that spent one day at the lowest value of AFG NPP in our study area (0 g C m^{-2} y^{-1}) would increase its daily survival rate to 0.9951 (Table 4.3). In contrast, spending one day at the 99th percentile value of AFG NPP in our study area (486 g C m^{-2} y^{-1}) would decrease daily survival rate to 0.9945. Because the effect on survival probability is cumulative, after 10 days in the minimum or maximum AFG NPP, daily survival probability would be 0.9961 or 0.9873, respectively (Table 4.3). We recorded mule deer juveniles only in lower values of AFG NPP, where survival was highest (Table 4.2).

Slope also had a negative effect on juvenile mule deer survival (mean -0.0106, 95% BCI -0.0171 – -0.0039), indicating that survival decreased in areas with steeper slopes. Unlike with AFG NPP, we recorded mule deer juveniles across all values of slope in our study area (Table 4.2).

In contrast to AFG NPP and slope, the two variables of elevation and shrub NPP had positive effects on survival, showing that survival increased at higher elevation and with higher shrub NPP. The effect sizes of elevation and shrub NPP were comparable, but elevation had a slightly stronger effect on survival (mean 0.0065, 95% BCI -0.0003 – 0.0131). Although credible interval of elevation overlapped 0, 97% of the posterior showed a positive effect. Shrub NPP had a slightly smaller positive effect on survival (mean 0.0061, 95% BCI -0.0019 – 0.0146), with 93% of the posterior distribution showing a positive effect. Mule deer juveniles were recorded at all elevations in our study area, but they remained in the smaller values of shrub NPP, using values from 0 – 81 g C m^{-2} y^{-1}, as compared to the range of 0 – 279 g C m^{-2} y^{-1} in the study area (Table 4.2).

Drought (PDSI) and perennials (PFG NPP) had no measurable effect on mule deer juvenile survival, as their posterior distributions overlapped 0 to a high degree. Mule deer juveniles used the full range of possible PFG NPP in our study area and all but the wettest values of PDSI, meaning they experienced a wide range of conditions from extreme drought to extreme wet (Table 4.2).

White-tailed deer juveniles

Mean daily survival of white-tailed deer juveniles was 0.9990 (95% BCI 0.9982 – 0.9995) and mean 6-month survival was 0.833 (95% BCI 0.726 – 0.910). This was considerably higher than survival probability of mule deer juveniles.

We found no evidence of an effect of any of our habitat variables on survival of white-tailed deer juveniles (Figure 4.3b). The 95% credible intervals for all habitat variables included 0, and the posterior distributions were not weighted to either side of 0. Each posterior had between 54-82% of its distribution on one side of 0, demonstrating no support for a meaningful effect of any habitat variable.

Mule deer adult females

Mean daily survival for mule deer adult females was 0.9994 (95% BCI 0.9993 – 0.9996). Mean annual survival was 0.82 (95% BCI 0.78 – 0.86).

There was some evidence of an effect of drought on mule deer adult female survival, with the posterior overlapping 0 but 92% of the posterior indicating a positive effect of PDSI (mean 0.0016, 95% BCI -0.0007 – 0.0039; Figure 4.3c). This indicated that wetter conditions increased survival and drier areas decreased survival. Additionally, there was some weak evidence of an effect on survival of PFG NPP and AFG NPP, with 87% and 88% of the posteriors, respectively, showing a negative effect. The small negative effect of PFG NPP (-0.0016, 95% BCI -0.0043 – 0.0013), showed that survival decreased in areas with higher NPP of perennial forbs and grasses. AFG NPP also showed a negative effect on survival (mean -0.0006, 95% BCI -0.0015 – 0.0005), but the effect size was very small, so the evidence of an effect of annual forbs and grasses on survival was very weak. The small effect sizes translated to smaller changes in daily and annual survival than predicted for mule deer juveniles (Table 4.4).

White-tailed deer adult females

Mean daily survival for white-tailed deer adult females was 0.9990 (95% BCI 0.9988 – 0.9992), which was equal to survival of juveniles. Mean annual survival was 0.69 (95% BCI 0.64 – 0.74).

There was evidence of an effect of slope, drought, and AFG NPP on white-tailed deer adult survival, with approximately 100% of each posterior showing a positive effect for each (Figure 4.3d; Table 4.5). The effect sizes of slope and AFG NPP were comparable, and the effect of drought was smaller. First, slope had a small positive effect on survival (mean 0.0046, 95% BCI 0.0020 – 0.0071), indicating that survival increased at steeper slopes. The positive effect of AFG NPP (mean 0.0042, 95% BCI 0.0012 – 0.0073) indicated that survival increased with higher NPP of annual forbs and grasses. PDSI had a smaller positive effect on survival (mean 0.0026, 95% BCI 0.0010 – 0.0043), indicating that survival increased in wetter conditions and decreased in drier conditions. There was no evidence of an effect of elevation, PFG NPP, or shrub NPP, as no more than 65% of any of their posteriors was on one side of 0.

Habitat quality maps

Using the mean estimated habitat variable effects for each species and age class, we mapped predicted habitat quality across our study area at a daily resolution (Figure 4.4). Because maps used mean effects, they did not reflect the variation in parameter estimates.

Discussion

Using the SHQ model, we were able to quantify the long-term effects of habitat on sympatric populations of mule deer and white-tailed deer. We measured the varying effects on survival of topography, drought, and nutritional resources via the amount that each resource increased or decreased survival. Building on traditional survival models, this approach provided a new way to account for long-term and cumulative effects of habitat without needing to define the time scale of lag effects. The SHQ model takes full advantage of GPS collar data and extensive, fine-scale remote sensing data that are recent additions to the wildlife field. The results shed new light on how to define habitat quality for a generalist species.

Overall, we found that juvenile white-tailed deer and adult female mule deer were able to use a broad spectrum of habitat values with little impact on survival, as demonstrated by posterior distributions overlapping 0 (Figure 4.3). Although these two groups showed little response to habitat on average, the large variances for white-tailed deer juveniles indicated that individuals had widely variable responses to habitat, while individual adult female mule deer consistently had little to no response to different habitat variables. For juvenile white-tailed deer, this could indicate that some unmeasured variation between individuals, such as body weight, changed the patterns of habitat needed to meet nutritional demands. Alternatively, our small number of recorded mortalities for white-tailed deer juveniles may have prevented us from estimating any effects precisely. In contrast, mule deer adult females' consistent lack of response to habitat indicated that stochastic or short-term factors (such as vehicle collisions or extreme weather events) may have played a larger role in their survival than the long-term effects of nutrition and habitat condition did. Mule deer adult female survival was consistent with normal values range-wide (Forrester and Wittmer 2013), which indicated that sufficient quality habitat was available in our study area to meet their nutritional demands. In environments that are not limiting (e.g., available forage meets nutritional demands, no excessive harvest, weather within normal range), adult female mule deer survival may not be predictable from environmental variables. It is possible to formulate the SHQ model to investigate short-term effects in addition to the long-term factors, so future studies may want to incorporate the instantaneous risk of predation, vehicle collision, or hunting in the analysis.

Our other two groups – mule deer juveniles and white-tailed deer adult females – showed stronger responses to habitat, as indicated by larger effect sizes and posteriors not overlapping 0. Mule deer juvenile variances were larger than variances for adult females of either species, contributing additional evidence that inter-individual survival responses to habitat are more variable for juveniles than for adults. However, it is also possible that the larger variances for juveniles was a product of their shorter encounter histories (approximately 6 months, compared to 1 year for adults). Because survival of mule deer juveniles and white-tailed deer adult females was more strongly affected by habitat than survival of white-tailed deer juveniles or mule deer adult females was, predicted habitat quality throughout the study area was more variable for the former two groups than the latter. The effects of habitat on survival of these two groups indicated that habitat quality was more variable throughout the study area than for white-tailed deer juveniles and mule deer adult females.

When comparing the two species, we found little evidence that any habitat variable had a consistent positive or negative effect for age classes of both species. Variables that registered as important for one species imposed either the opposite effect or no effect on the other species. For example, AFG NPP had a strong negative effect on mule deer juveniles but neutral effect on white-tailed deer juveniles and a positive effect on white-tailed deer adult females. Drought (PDSI) was the only variable that potentially affected adult females in the same direction, although the evidence of an effect on mule deer adult females was weak.

From the six environmental variables we measured, we found that topography (elevation and slope) formed a key distinction between mule deer and white-tailed deer, which is consistent with studies elsewhere in their sympatric range (Staudenmaier et al. 2021). The first topographical factor, elevation, had a positive effect on mule deer juvenile survival but neutral effect on every other group. Higher elevation is routinely used to describe mule deer habitat, and our results lend more evidence in support of this (Martinka 1968, Anthony and Smith 1977, Anderson et al. 2012). Our study area was relatively flat and low-elevation compared to other areas in mule deer range, yet within it we found that mule deer juveniles survived better at higher elevations than the surrounding area. The second topographical factor, slope, was more surprising; generally, mule deer are thought to prefer higher slopes than white-tailed deer (Avey 2003, Staudenmaier 2021), although we found the opposite: steeper slopes had a negative effect on mule deer juveniles but positive effect on white-tailed deer adult females (and was neutral for other groups). There are two potential biological drivers of this pattern in our study area. First, slope is that our study area was relatively flat, with the highest slope measuring 20°. Steeper slopes were associated with the few rugged buttes in our study area but also with river bottoms, which are generally considered white-tailed deer habitat (Whittaker and Lindzey 2004). Second, it has been shown that mule deer prefer to forage in low-slope areas but use steeper slopes to flee coyote predation (Lingle 2002). Under this hypothesis, we would predict a negative effect of slope on long-term survival (i.e., nutrition) but a positive effect on short-term survival (i.e., predation). Although we did not measure short-term survival, we did find evidence of a long-term negative effect.

Further evidence for this hypothesis was that we found a the negative effect only in mule deer juveniles, which are more susceptible to predation than adults.

We recorded a wide range of PDSI values in our study area, from extreme drought to extreme wet (see Chapter 2, Figure 2.3). Both age classes of both species used comparable values of PDSI; all groups were found in a wide range of values except the two extremes. Drought had the largest effect on white-tailed deer adult females, indicating that white-tailed deer were more sensitive to drought than mule deer. Drought conditions lower the abundance and quality of deer forage, which may affect white-tailed deer disproportionately because mule deer are able to meet nutritional demands with lower-quality food (Staudenmaier et al. 2022). Additionally, drought conditions increase the chance of outbreak of epizootic hemorrhagic disease (Christensen et al. 2020), which tends to be deadlier for white-tailed deer than mule deer (Hoff et al. 1973). If drought conditions increase across mule deer habitat, mule deer may have a competitive advantage over white-tailed deer by tolerating a wider range of climatic conditions.

We found little or no effect of perennial forbs and grasses on survival of any group. Perennial forb species make up more of a deer’s diet than annuals, but grasses make up a very small percentage of the diet (Everitt and Draw 1974). If PFG NPP values were mostly driven by grasses rather than forbs (which we could not evaluate with our data), we would indeed expect to find little to no effect on survival. We would also expect to see no effect if all values of PFG NPP in the study area met the basic nutritional needs of deer, because this resource would not be limiting for survival. Some recorded values of PFG NPP were unreasonably high, which may indicate that the remote sensing dataset was insufficient for measuring PFG NPP in our study area. Globally, the highest

NPP in rainforests is less than 1000 g C m^{-2} yr^{-1} (Yinpeng and Jinjun 2001), but our highest values of PFG NPP were above 4000 g C m^{-2} yr^{-1}. We suspect that the unrealistically high values were a result of algorithm not accounting for satellite reflection from bare ground or potentially agriculture.

Net primary productivity of annual forbs and grasses increased white-tailed deer adult female survival but decreased mule deer juvenile survival and potentially decreased adult mule deer survival. Forbs are an important part of a deer's diet, so it was surprising that mule deer juveniles were strongly negatively affected by AFG NPP (Everitt and Draw 1974). The negative effect of AFG on mule deer juveniles could indicate that areas with high values of AFG NPP were low-quality mule deer habitat for some other reason, perhaps due to competition from white-tailed deer or to increased predation, which would affect juveniles more than adults. Similar to PFG NPP, we recorded some extremely high values of AFG NPP, which could have directed the strong effect. Yet unlike PFG NPP, the large values were outliers in the top 1% of the available values. Upon close inspection of our remote sensing data, the large values of AFG NPP appeared in a small area where bare soil was visible in badlands-type formations. We recorded juveniles only at lower, reasonable values of AFG NPP, so it is unlikely that the remote sensing errors drove our results. Furthermore, mule deer juveniles were found in the smallest range of AFG NPP of any species and age class, indicating selection for the values where their survival probability was highest, which was evidence that the effect was real.

Shrub NPP had a positive effect on juvenile mule deer survival but no effect on any other group. Shrubs are important browse for both species and make up the bulk of their diet (Berry et al. 2019), so it was surprising that three groups showed no effect.

These results may indicate that sufficient values of shrubs were available to three groups but not so for mule deer juveniles. Although mule deer juveniles responded positively to shrub NPP, they used the smallest range of values of any of our deer groups. This potentially indicated that high values of shrub NPP were inaccessible for some reason, for instance, due to higher predation rates in these areas.

We chose to investigate the effects of six habitat variables we hypothesized would be influential on deer survival, but there are additional factors that could be incorporated into the model. For example, other resources that could affect long-term survival include agricultural crops and hard winters. As the first test of the new SHQ model, we chose to focus only on continuous variables with a wide range of values across the study area, whereas both agriculture and extreme cold were rare in our study area and represented by categorical covariates. However, with appropriate prior distributions designed for missing data of each, these and other factors could be incorporated into the SHQ model in the future. Additionally, as more high-quality remote sensing data becomes available, we could increase the accuracy of our estimates with finer-scale variables. For example, all of our NPP values (PFG, AFG, and shrub) were calculated on an annual basis, so we did not have the temporal resolution to capture how NPP changed throughout the year. In reality, cells with high NPP values did not necessarily have high NPP in every season. When finer temporal resolution datasets become publicly available, the SHQ model could more accurately assess how NPP affects survival throughout the year.

Throughout the analysis, we assumed that the underlying equation describing habitat quality did not differ over time. This played out in two ways. First, we assumed that each environmental variable was equally important throughout the year. Future studies may want to differentiate between resource needs at different times of year, including the rut, winter, and post-parturition, as nutritional needs may vary with different physical demands. We also assumed that habitat needs did not vary by year. Under this assumption, we limited our analysis to daily survival from January 1 to December 31, and individuals that were alive in multiple years were included as independent individuals. This eased the computational load of the model, as run time increased non-linearly with the number of occasions.

Two potential avenues of research could increase the biological reality of the SHQ model for future applications. First, The SHQ model is a fully cumulative model where every past experience contributes to an individual's current survival probability. Biologically speaking, there may be a cutoff when past experience is no longer relevant to a deer's probability of survival. It is possible that the SHQ model could incorporate a moving window that would allow only recent experiences (e.g., six months) to dictate survival probability. This may also ease the computational load and allow long-lived individuals to be included as a single, continuous encounter history. Second, we defined habitat patches (i.e., grid cell sizes) based on population-wide daily movement patterns, which may not perfectly represent the environmental conditions used by an individual animal on a particular day. Habitat use may occur at a finer scale than we were able to capture, and there is likely inter-individual variation and temporal variation in space use. A future extension of the SHQ model might use fine-scale GPS data and movement modeling to define habitat patch size by individual and allow it to vary over time.

While the SHQ model allows inference to the variation in responses to different resources, it is difficult to visualize that variation in a predictive map. Maps using mean parameter estimates may not accurately depict habitat quality if the inter-individual variation in survival responses is high. For example, all habitat variables for white-tailed deer juveniles had wide posterior distributions that spanned many potential values, from positive to negative. Using the mean values, our map (Figure 4.4c) indicated many areas of low-quality habitat for white-tailed deer juveniles, but this may not be an accurate representation of habitat quality, as our results indicate that white-tailed deer juveniles tolerated a wide range of habitat values with little effect on survival. Additionally, white-tailed deer juvenile survival was higher than mule deer juvenile survival, but the visualization of results indicated that much more of our study area should be considered poor quality habitat for white-tailed deer compared with mule deer. With more variation in responses, visualizing habitat quality from the SHQ model becomes more challenging, and accurately depicting variability could be an avenue for future research efforts.

Managers trying to manage for large mule deer populations and smaller white-tailed deer populations have two critical tools at their disposal: harvest regulation and habitat management. In many areas, harvest regulation is insufficient to achieving these goals for several reasons. First, in highly abundant white-tailed deer areas, it can be hard to harvest enough deer to change the population size due to declines in hunter numbers, restricted access on private lands, and focus by hunters on buck harvest rather than female harvest (Vercauteren and Hygnstrom 2011, Vercauteren et al. 2011). Second, mule deer populations tend to be limited by recruitment of juveniles (Carpenter 1997, Gaillard et al. 1998), so manipulating harvest of adults may not have a strong effect on population trajectory, especially if harvest is focused on adult males. However, habitat management can increase overwinter survival of mule deer fawns (Bergman et al. 2014), so habitat management may be a better tool for achieving population goals. A complete understanding of what makes up high-quality mule deer habitat as opposed to white-tailed deer habitat is crucial for designing management interventions.

Managers aiming to increase mule deer populations through habitat management should likely focus on the factors most important for mule deer juvenile survival (Carpenter 1997). In our study area, these factors were slope, elevation, shrubs, and annuals. While managers cannot change slope or elevation, it may be possible to manage for more shrubs and fewer annual forbs and grasses. In particular, more shrubs and fewer annual forbs and grasses in areas of higher elevation and lower slope could be most beneficial. Higher elevations in our study area were often associated with butte formations, which also have low slopes on top. These formations were typically on public land, so this could be a potential avenue for habitat management without the need for landowner buy-in to incentive programs.

Through our test of the SHQ model on mule deer and white-tailed deer, we found that the model can provide a thorough understanding of habitat quality as it relates to population demographic rates. Furthermore, the predictive maps of habitat quality can help conservationists highlight areas of conservation priority. Particular focus of habitat management interventions should be placed on resources that are important to survival (i.e., effect sizes on survival are large with small variation), are easy to manipulate, and have abundant poor quality patches.

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Tables

Table 4.1. Number of new GPS collars deployed annually. Collars functioned for multiple years, so sample sizes in 2020 and 2021 were larger than column *n* would indicate.

Year	Species	Age class	n
2019	Mule Deer	Adult female	105
2019	White-tailed Deer	Adult female	106
2020	Mule Deer	Adult female	22
2020	Mule Deer	Juvenile	111
2020	White-tailed Deer	Adult female	18
2020	White-tailed Deer	Juvenile	112
2021	Mule Deer	Juvenile	107
2021	White-tailed Deer	Juvenile	109

Table 4.2. Summary of habitat variables the DAU 1 study area from January 2019 – December 2021 and recorded use by collared mule deer and white-tailed deer juveniles and adult females.

Variable	Species	Mean	SD	Min	Max
AFG NPP (g C m^{-2} y^{-1})	Study area	101	124	0	2955
	Mule deer juvenile	52	41	1	289
	White-tailed deer juvenile	66	58	0	319
	Mule deer adult female	114	161	0	2955
	White-tailed deer adult female	102	93	0	1611
Elevation (m)	Study area	854	103	488	1211
	Mule deer juvenile	844	99	580	1174
	White-tailed deer juvenile	843	102	571	1192
	Mule deer adult female	859	108	586	1187
	White-tailed deer adult female	851	99	35	1176
[1] PDSI	Study area	0.7	3.36	-5.2	14
	Mule deer juvenile	1.2	3.9	-3.6	10.7
	White-tailed deer juvenile	1.4	3.8	-3.7	10.5
	Mule deer adult female	0.7	3.3	-4.8	11.7
	White-tailed deer adult female	0.6	3.2	-4.8	11.0
PFG NPP (g C m^{-2} y^{-1})	Study area	2384	655	0	4956
	Mule deer juvenile	2285	481	48	3910
	White-tailed deer juvenile	2252	639	0	3910
	Mule deer adult female	2442	617	24	4469
	White-tailed deer adult female	2365	706	0	4334
Shrub NPP (g C m^{-2} y^{-1})	Study area	125	15.3	0	279
	Mule deer juvenile	11	15	0	81
	White-tailed deer juvenile	8	13	0	115
	Mule deer adult female	17	25	0	146
	White-tailed deer adult female	15	21	0	203
Slope (°)	Study area	4.1	2.6	0	20
	Mule deer juvenile	5.1	2.7	0	19
	White-tailed deer juvenile	3.0	1.8	0	18
	Mule deer adult female	5.1	2.9	0	20
	White-tailed deer adult female	3.2	2.0	0	20

[1] PDSI values range from -15 (driest) to 15 (wettest)

Table 4.3. Effects of four habitat variables on survival probability of an individual mule deer juvenile. Calculations are based on an individual starting with mean daily survival probability (0.9950), and spending 1, 2, and 10 days at the minimum and maximum values of each habitat variable, assuming all other variables are held at their mean. To aid in interpretation, 6-month survival probabilities projected from the daily rates are reported in parentheses and printed in red to differentiate from annual survival in Tables 4.4 – 4.5. Values that increase over time are highlighted in yellow.

Habitat value	Time spent	AFG NPP[1]	Elevation	Slope	Shrub NPP
Minimum	1 day	0.9951 (0.41)	0.9949 (0.39)	0.9951 (0.41)	0.9950 (0.40)
	2 days	0.9952 (0.42)	0.9948 (0.38)	0.9952 (0.41)	0.9950 (0.40)
	10 days	0.9961 (0.49)	0.9937 (0.31)	0.9958 (0.46)	0.9948 (0.38)
Maximum	1 day	0.9945 (0.37)	0.9951 (0.41)	0.9947 (0.38)	0.9953 (0.43)
	2 days	0.9940 (0.33)	0.9952 (0.42)	0.9943 (0.35)	0.9957 (0.45)
	10 days	0.9873 (0.10)	0.9960 (0.48)	0.9905 (0.18)	0.9976 (0.64)

[1] Used 99th percentile rather than maximum for AFG NPP

Table 4.4. Effect of habitat variables on survival probability of an individual mule deer adult female. Calculations are based on an individual starting with mean daily survival probability (0.9994), and spending 1, 2, and 10 days at the minimum and maximum values of each habitat variable, assuming all other variables are held at their mean. To aid in interpretation, annual survival probabilities projected from the daily rates are reported in parentheses. Values that increase over time are highlighted in yellow.

Habitat value	Time spent	PDSI	PFG NPP	AFG NPP[1]
Minimum	1 day	0.9994 (0.82)	0.9994 (0.82)	0.9994 (0.82)
	2 days	0.9994 (0.82)	0.9995 (0.82)	0.9994 (0.82)
	10 days	0.9994 (0.81)	0.9995 (0.83)	0.9994 (0.82)
Maximum	1 day	0.9994 (0.82)	0.9994 (0.82)	0.9994 (0.82)
	2 days	0.9995 (0.82)	0.9994 (0.82)	0.9994 (0.82)
	10 days	0.9995 (0.83)	0.9994 (0.81)	0.9994 (0.82)

[1] Used 99th percentile rather than maximum for AFG NPP

Table 4.5. Effect of habitat variables on survival probability of an individual white-tailed deer adult female. Calculations are based on an individual starting with mean daily survival probability (0.9990), and spending 1, 2, and 10 days at the minimum and maximum values of each habitat variable, assuming all other variables are held at their mean. To aid in interpretation, annual survival probabilities projected from the daily rates are reported in parentheses. Values that increase over time are highlighted in yellow.

Habitat value	Time spent	AFG NPP[1]	PDSI	Slope
Minimum	1 day	0.9990 (0.69)	0.9990 (0.69)	0.9990 (0.69)
	2 days	0.9990 (0.69)	0.9990 (0.69)	0.9990 (0.69)
	10 days	0.9989 (0.68)	0.9989 (0.68)	0.9989 (0.67)
Maximum	1 day	0.9990 (0.69)	0.9990 (0.69)	0.9990 (0.70)
	2 days	0.9990 (0.70)	0.9990 (0.69)	0.9990 (0.70)
	10 days	0.9991 (0.72)	0.9991 (0.71)	0.9992 (0.75)

[1] Used 99th percentile rather than maximum for AFG NPP

Figures

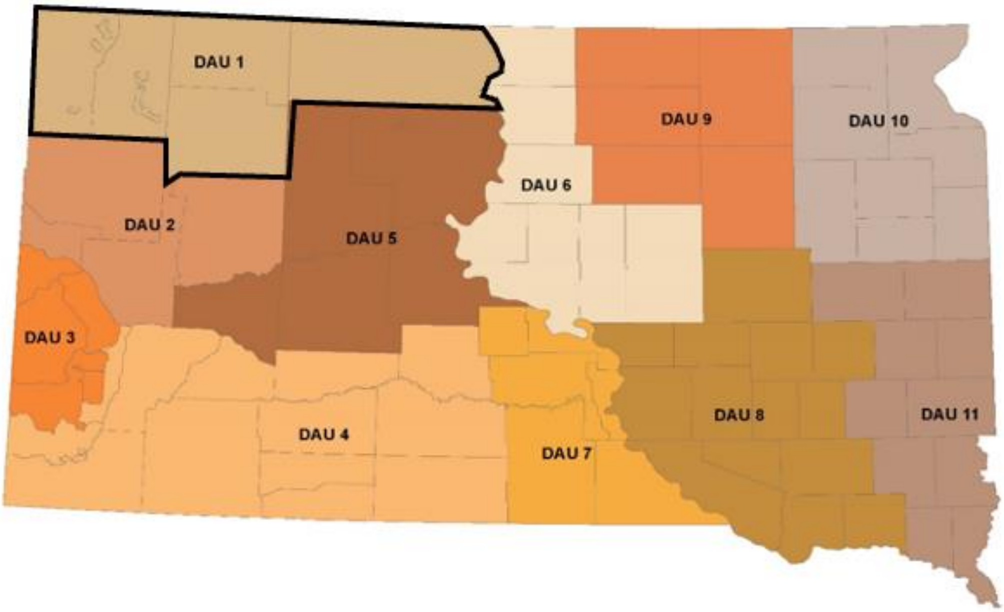

Figure 4.1. Data analysis units (DAUs) in South Dakota, USA, with our study area, DAU 1, outlined in black.

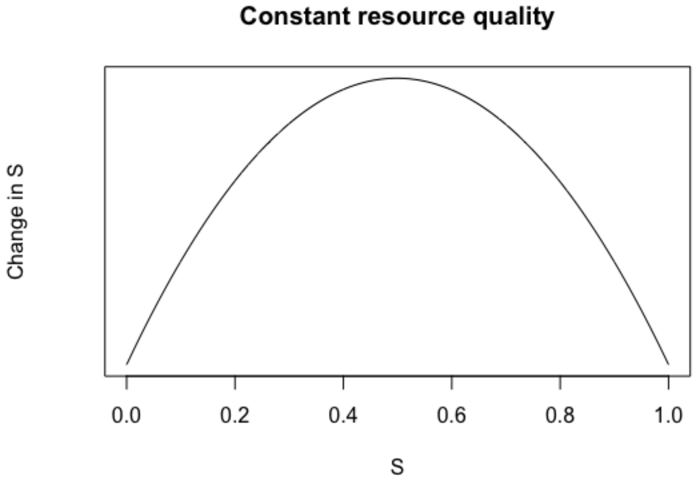

Figure 4.2. Due to the logit transformation, resource quality has a larger effect on individuals with survival probability near 0.5 than near either 0 or 1. Two individuals encountering the same resource will likely experience the effect size differently.

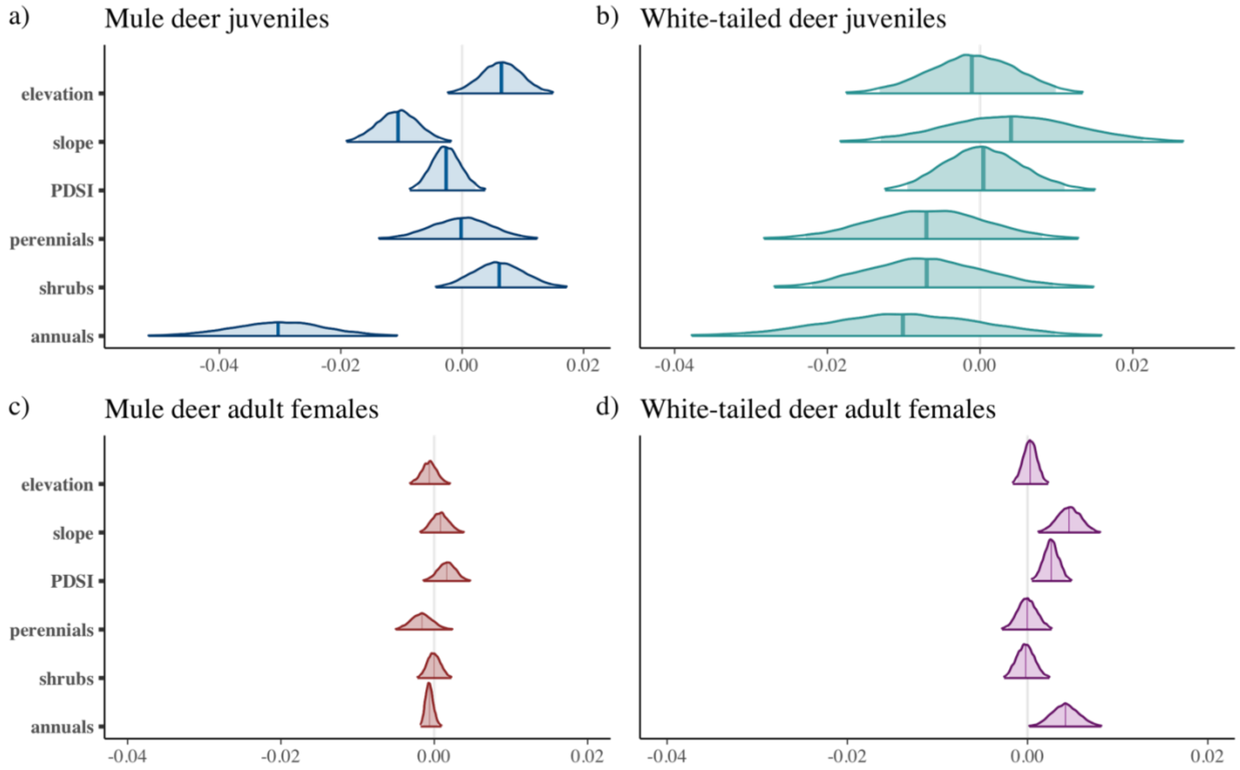

Figure 4.3. Posterior distributions for effects of habitat variables on daily survival of mule deer and white-tailed deer juveniles (<1 yr) and adult females (>1 yr). Mean estimates represented by colored vertical lines and 95% Bayesian Credible interval shown by shaded areas.

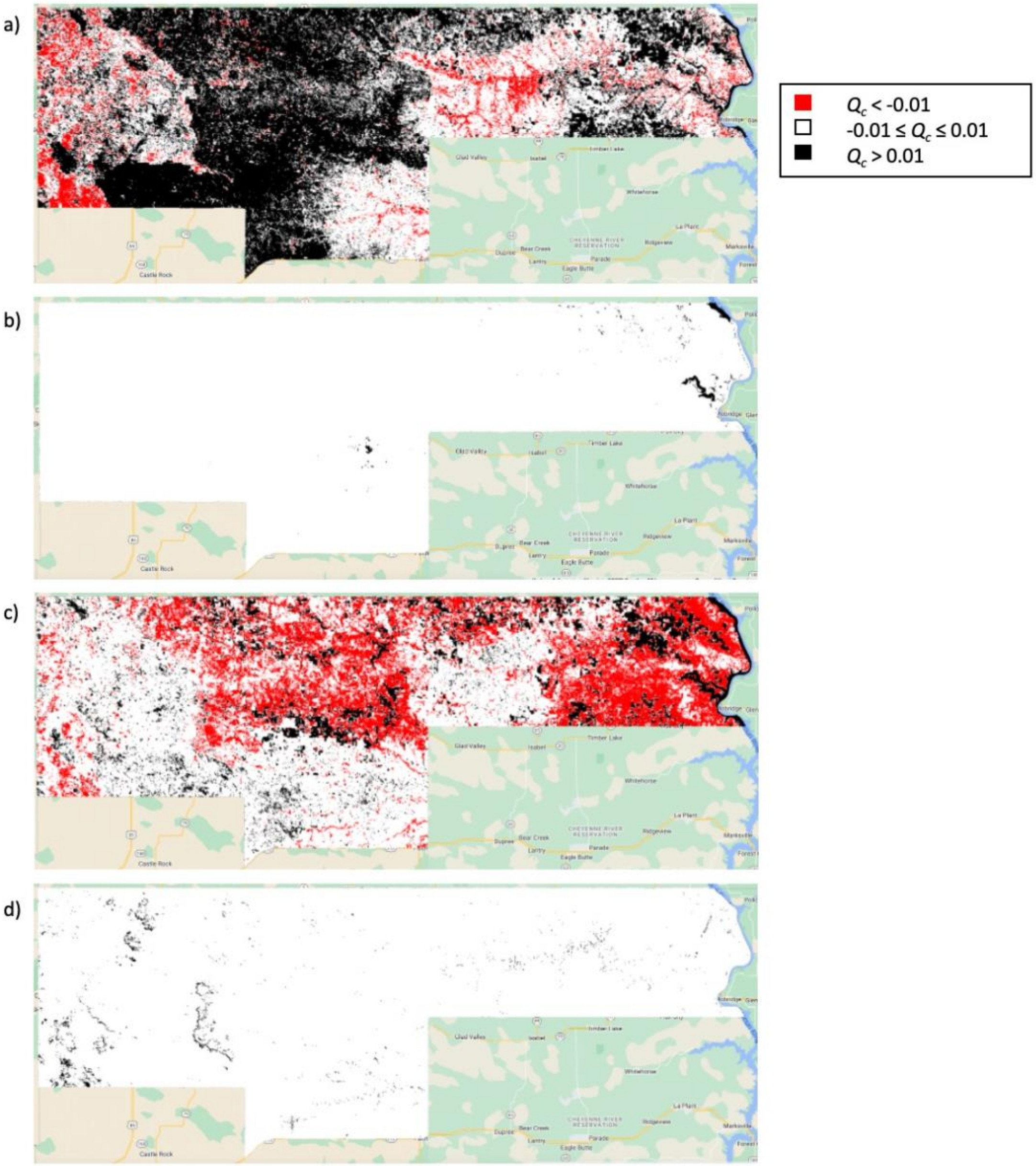

Figure 4.4. Predicted habitat in our study area. Example shown for Feb. 4, 2020 for a) mule deer juveniles, b) mule deer adult females, c) white-tailed deer juveniles, and d) white-tailed deer adult females, using mean effect size of six environmental variables. For visualization, habitats were grouped into poor (Q_c < -0.01), neutral (-0.01< Q_c <0.01), and high (Q_c > 0.01) quality.